# Estimating colony age from colony size in encrusting cheilostomes

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## ABSTRACT

The goal of this study is to develop a method of estimating colony age in encrusting cheilostomes from colony size. This will be useful for estimating colony age of small encrusting epibiotic bryozoans on ephemeral motile host animal substrates (e.g., exoskeletons of crabs that are susceptible to molting). Colony age (i.e., number of days) was modelled from colony size (i.e., number of zooids) from data collected by Xixing *et al.* (2001) on five cheilostome species grown in the laboratory. The growth of each species was measured in two different seasons for a total of 10 growth curves. The curves were best modelled by the following power function: $y = 0.2053x^{2.2663}$ (y = number of zooids, x = number of days, $R^2 = 0.97$). This function was then used to estimate the ages of encrusting epibiotic cheilostome bryozoan colonies from the author's previous studies on extant and extinct epibiotic bryozoans found on ephemeral motile host animal substrates. When using these kinds of predictive growth curves, it is important to stress that bryozoan growth rates are a function of several variables and so an estimated colony age range is recommended rather than simply a single "best guess" age.

## INTRODUCTION

Of all research on bryozoan growth rates, encrusting colonies have received the most attention. This is most likely because they are more easily grown in both the laboratory and field and their more two-dimensional nature is more easily measured than other more three-dimensional zoarial morphologies such as erect colonies (Smith 2007, 2014; Smith and Key 2019). This study focuses on growth rates in encrusting bryozoans. Early work on measuring growth rates of encrusting bryozoan colonies began with Lutaud (1961) on the best-documented species, *Membranipora membranacea*. Since then, numerous studies have examined the various factors affecting bryozoan colony growth rates (Table 1).

In studies of encrusting epibiotic bryozoans living on host animals, being able to estimate colony age from colony size would useful for constraining the age of the host. Some motile host animals provide only ephemeral substrates due to skin shedding (e.g., sea snakes: Key *et al.* 1995) or molting of their exoskeleton (e.g., arthropods: Key and Barnes 1999; Key *et al.* 1996a, b, 1999, 2000, 2013, 2017). Knowing colony age would help constrain intermolt duration of the hosts, especially fossil hosts (e.g., Gili *et al.* 1993; Key *et al.* 2010, 2017). Therefore, the goal of this study is to model encrusting cheilostome colony age from colony size as quantified by the number of zooids which can be more easily measured on fossil host exoskeletons.

I follow the terminology of Wahl (1989) and refer to the motile hosts as basibionts (i.e. the host substrate organisms) and the bryozoans as epibionts (i.e. the

**Table 1. Known variables that affect encrusting bryozoan colony growth rates.**

| Variable | Reference(s) |
|---|---|
| Food availability | Winston 1976; Cancino and Hughes 1987; Hughes 1989; O'Dea and Okamura 1999; Hermansen *et al.* 2001 |
| Competition for food along the margins of neighboring colonies | Buss 1980; McKinney 1992, 1993 |
| Temperature | O'Dea and Okamura 1999; Amui-Vedel *et al.* 2007 |
| Water flow velocity | Hughes and Hughes 1986; Cancino and Hughes 1987; Pratt 2008; Sokolover *et al.* 2018 |
| Availability of substrate space with adjacent colonies competing for space | Stebbing 1973; Yoshioka 1982 |
| Availability of substrate space without adjacent colonies | Winston and Hakansson 1986 |
| Presence of associated fauna | Cocito *et al.* 2000 |
| Relative investment in sexual reproduction vs. asexual colony growth | Harvell and Grosberg 1988; Hughes 1989; Herrera *et al.* 1996 |
| Development of anti-predatorMorphologies | Harvell 1986, 1992; Grünbaum 1997 |
| Genetic variation | Bayer and Todd 1996 |

sessile organisms attached to the basibiont's outer surface without trophically depending on it). Following the terminology of Taylor and Wilson (2002), I will focus on epibionts as opposed to endosymbionts as the bryozoans are ectosymbionts or episkeletozoans inhabiting the surface of their basibiont host.

## MATERIALS AND METHODS

To model growth in encrusting bryozoans, the rich growth rate datasets from Xixing *et al.* (2001) were used. Their tables 14–15, 18–20 list growth rates of five fouling marine cheilostome species raised on artificial substrates in the laboratory (Table 2). They are all exclusively encrusting species except for *Membranipora grandicella* and *Watersipora subtorquata* which can become erect during later astogeny, but these species only exhibited encrusting growth during the study. Xixing *et al.* (2001) report data from two different growth periods in the summer of 1995 (i.e., the slightly cooler months of May–June and the slightly warmer months of July–August) for each species. Small colonies, consisting of ancestrulae, were collected on panels in 2–8 m depth and transported to the laboratory. There were

collected from the mouth of Jiaozhou Bay offshore of Qingdao, China located on the Yellow Sea at ~36°01'N, 120°20'E. The authors tried to mimic the conditions in the coastal waters of Qingdao as far as temperature, salinity, and food availability, but not the presence of predators. During the laboratory experiments, salinity was held constant at 32 ppt. Water temperatures for the May–June experiments ranged from 15 to 24°C, while in July–August they ranged from 24 to 28°C. The bryozoans were fed a diet of $1-2\times10^5$ cells twice per day of unicellular marine microalgae consisting of *Platymonas* sp. 1048, *Isochrysis galbana* 3011, and *Phaeodactylum tricornutum* 2038. The authors reported that other than the effect of predators, the growth rates in the laboratory paralleled those observed on artificial and natural substrates offshore. Epibionts on ephemeral motile basibionts experience almost no predation (Ross 1983). Therefore, Xixing *et al.*'s (2001) growth rates should be generally representative of encrusting epibiont cheilostomes growing in temperate marine environments. The authors report the number of zooids by the number of days of growth (Table 2). The number zooids counted per colony ranges from 391 to 1644 (mean: 744, standard deviation: 325

zooids). The number of days of growth ranges from 30 to 66 (mean: 44, standard deviation: 14 days).

The rate of asexual zooid replication increases with colony size in many bryozoan species (Lutaud 1983; Winston and Jackson 1984; Hughes and Hughes 1986; Lidgard and Jackson 1989). Therefore, the rate of growth in the number of zooids is non-linear. There are five commonly used curves to model such growth: exponential, power, Gompertz, logistic, and Bertalanffy (Kaufmann 1981). The standard graphing practice of Kauffman (1981) was followed with the horizontal (x) axis being time and the vertical (y) axis being size. The best fit curve for each of Xixing *et al.*'s (2001) 10 laboratory experiments was calculated.

## RESULTS AND DISCUSSION

The power curve model had the highest $R^2$ values (mean = 0.97, range: 0.93–0.98, standard deviation = 0.17) for each of the 10 data sets (Fig. 1, Table 2). The equation of a power growth curve is $y = ax^b$. In this study, y = colony size (i.e., the number of zooids), x = time (i.e., the number of days of growth), a = value of the coefficient in the power function (a.k.a., the proportionality constant), and b = value of the exponent (i.e., the power to which x is raised). Combining the data from all five species, the mean growth curve for the cooler late

spring–early summer months (i.e., May–June) is $y = 0.1522x^{2.3490}$, and the mean growth curve for the warmer late summer months (i.e., July–August) is $y = 0.2583x^{2.1836}$ (Fig. 2). The mean growth curves are not significantly different between May–June and July–August (t-Tests, coefficient and exponent in power function, $P = 0.36$ and $P = 0.27$, respectively). Therefore, all 10 curves were combined into the mean growth power curve of $y = 0.2053x^{2.2663}$ (Table 2).

The growth curves of the young colonies in this study lack the early steeply concave up, exponential start and late concave down end of a sigmoidal curve. Young colonies often show the early steeply concave up, exponential start (Winston 1976) whereas some longer lived encrusting bryozoans show a more sigmoidal growth curve (Hayward and Ryland 1975; Kaufmann 1981). The latter are better modelled by a Gompertz growth curve (Kaufmann 1981; Karkach 2006). Xixing *et al.* (2001, p. 785) noted the absence of this classic logarithmic increase in the number of zooids in the youngest part of the colonies, and the experiments were not run long enough to document any later astogenetic slowdown in growth. The species in this study always had a concave up growth curve best modelled by a power curve (Kaufmann 1981). The power function has been previously used to model growth in bryozoans (Hartikainen *et al.* 2014).
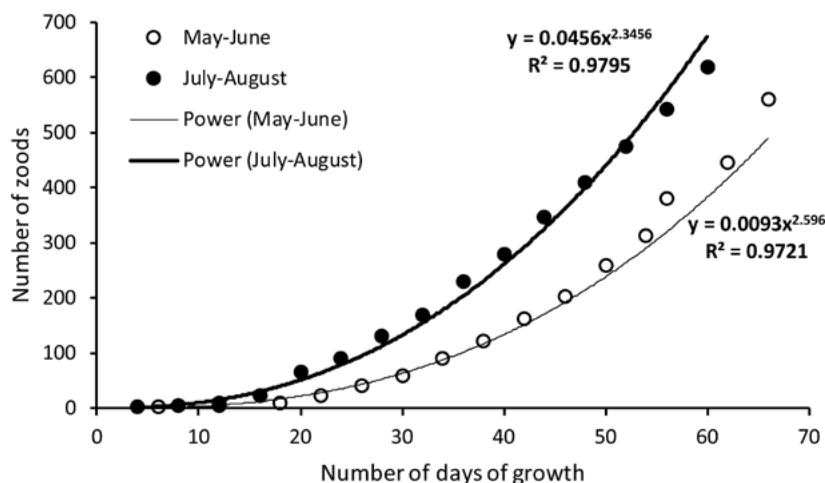


Figure 1. Growth curves for the cheilostome *Watersipora subtorquata*. Data from Xixing *et al.* (2001, table 20).

**Table 2. Summary growth rate data of encrusting cheilostome bryozoans grown in the laboratory by Xixing *et al.* (2001).**

| Table number in Xixing *et al.* (2001) | Species | Growth season | Total number of zooids counted | Total days of growth | Mean number of days between measurements | R² value | Value of coefficient in power function | Value of exponent in power function |
|---|---|---|---|---|---|---|---|---|
| 14 | *Membranipora grandicella* | May-June | 660 | 38 | 2.4 | 0.9765 | 0.0828 | 2.4255 |
| 14 | *Membranipora grandicella* | July-August | 929 | 32 | 2.0 | 0.9839 | 0.4999 | 2.1270 |
| 15 | *Electra tenella* | May | 633 | 30 | 2.0 | 0.9825 | 0.4625 | 2.0468 |
| 15 | *Electra tenella* | July | 1644 | 30 | 2.0 | 0.9773 | 0.2599 | 2.4721 |
| 18 | *Schizoporella unicornis* | May-June | 649 | 58 | 2.9 | 0.9555 | 0.0324 | 2.3412 |
| 18 | *Schizoporella unicornis* | July-August | 656 | 36 | 2.1 | 0.9838 | 0.2474 | 2.1258 |
| 19 | *Cryptosula pallasiana* | May | 702 | 30 | 2.0 | 0.9632 | 0.1740 | 2.3354 |
| 19 | *Cryptosula pallasiana* | July-August | 391 | 60 | 4.0 | 0.9299 | 0.2387 | 1.8476 |
| 20 | *Watersipora subtorquata* | May-June | 560 | 66 | 4.4 | 0.9721 | 0.0093 | 2.5960 |
| 20 | *Watersipora subtorquata* | July-August | 618 | 60 | 4.0 | 0.9795 | 0.0456 | 2.3456 |
| | | **Number:** | 10 | 10 | 10 | 10 | 10 | 10 |
| | | **Minimum:** | 391 | 30 | 2.0 | 0.9299 | 0.0093 | 1.8476 |
| | | **Mean:** | 744 | 44 | 2.8 | 0.9704 | 0.2053 | 2.2663 |
| | | **Maximum:** | 1644 | 66 | 4.4 | 0.9839 | 0.4999 | 2.5960 |
| | | **Standard deviation:** | 325 | 14 | 0.9 | 0.0161 | 0.1639 | 0.2135 |

Since the goal of this study is to estimate colony age of small encrusting cheilostome colonies on ephemeral hard substrates such as arthropod carapaces, the power curve is the best way to model the growth. Because the ephemeral substrates the basibionts produce do not provide long-lived substrates for bryozoans, I chose to model growth using higher temporal resolution, shorter duration growth studies. For example, Hayward and Ryland (1975, fig. 2) measured growth in *Alcyonidium hirsutum* for almost a year, so they took monthly measurements (i.e., roughly every 30 days). Most ephemeral basibiont substrates do not last that long due to the basibiont molting or shedding. The data from Xixing *et al.* (2001) included up to two months of growth data, but measurements were made on average every three days

(mean = 2.8, range = 2.0–4.4, standard deviation = 0.9 days). For larger/older colonies (e.g., *Alcyonidium hirsutum* in Hayward and Ryland (1975, fig. 2)), a more sigmoidal growth curve (e.g., Gompertz) may be more applicable than a power curve as used here.

To demonstrate the utility of the equations in Table 2, I applied them to previous studies where the number of zooids were reported for colonies encrusting basibionts that produce ephemeral substrates (Table 3). Ideally one would apply the predictive models to the same species as growth rates vary among species (Smith 2007, 2014; Smith and Key 2019), and to species growing in the same location and environmental conditions as growth rates vary in response to different environmental conditions (Table 1). Being this restrictive would be the most conservative approach but would greatly limit its

applicability. When using these equations to estimate colony age, these limitations must be kept in mind. But for the fossil record of small colonies encrusting crab carapaces, it is recommended to use the equations to bracket a range of colony ages to the nearest order of magnitude. Therefore, the equations were herein used to calculate a minimum, mean, and maximum estimated colony age (Table 3). One must also keep in mind that in fossils, colonies may not be completely intact, so some zooids may be missing from the count.

The calculated mean colony ages ranged from 6 to 31 days, depending on the size of the colony (Table 3). The calculated range in colony ages was 4–246 days (i.e., two orders of magnitude variation). This large range is not due as much to variation in growth rate, which are surprisingly constrained (Table 2) but is more due to variation in colony size. Colony size varies greatly depending on the host (Table 3), typically in proportion to host age and intermolt duration (Gili *et al.* 1993).

These colony age estimates also help constrain the duration of the host substrate between shedding or molting events, unless the host species experiences

terminal anecdysis. A few crab species do this (i.e., continue to live without molting after reaching sexual reproduction) (Abelló *et al.* 1990; Fernandez-Leborans, 2010). In those cases, minimum colony age is a more accurate way to estimate intermolt duration. Estimating epibiont bryozoan colony age is useful for fossil basibionts where intermolt duration is often impossible to constrain. For example, in trilobites with morphologically distinct developmental stages (e.g., Park and Choi 2011, fig. 4), the number of zooids counted in a colony on a fouled basibiont would indicate the minimum time since the last molt. In the hosts listed in Table 3, the minimum intermolt duration indicated by the minimum colony age varies from 4–14 days, a much more constrained range than 4–246 days. Of course, the estimated intermolt durations should be most accurate if restricting their use to Cenozoic fossil crabs fouled by cheilostomes as indicated in Table 3 as opposed to Paleozoic stenolaemates, for example.

In a microevolutionary fitness sense, the colonies must achieve sexual reproduction before the basibiont molts/sheds in order for the epibiotic relationship to
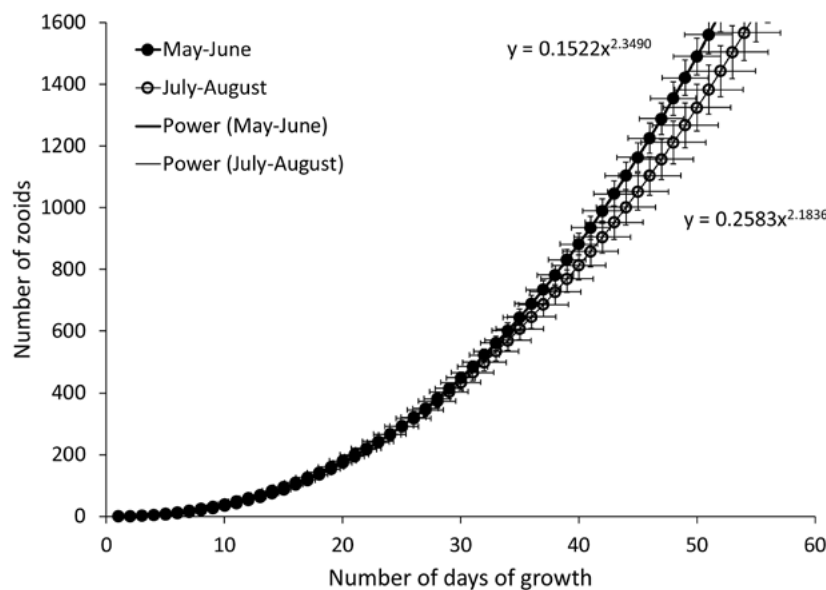


Figure 2. Mean growth curve for the cooler late spring-early summer months (i.e., May-June) and the warmer late summer months (i.e., July-August) averaged from the five cheilostome species in Table 2. Error bars indicate variation among species in each growth period.

**Table 3. Estimated ages of encrusting epibiotic cheilostome bryozoan colonies from author's previous studies. Colony ages were calculated from modelled growth curves based on the number of zooids per colony and the minimum, mean, and maximum power functions in Table 2.**

| Epibiont bryozoan species | Basibiont host species | Source | Geologic age | # of zooids | Colony age (days) | | |
|---|---|---|---|---|---|---|---|
| | | | | | Min. | Mean | Max. |
| *Arbopercula (Electra) angulata* | *Lapemis hardwickii* (sea snake) | Key *et al.* (1995) | Extant | 14-16 | 4 | 6-7 | 52-56 |
| *Arbopercula (Electra) angulata* | *Enhydrina schistosa* (sea snake) | Key *et al.* (1995) | Extant | 19-156 | 4-9 | 7-19 | 62-193 |
| *Acanthodesia* sp. | *Myra* sp. (crab) | Key *et al.* (2017) | Miocene | 22 | 4 | 8 | 67 |
| Indeterminate ascophoran | Indeterminate crab | Key *et al.* (2017) | Miocene | 35-243 | 5-11 | 10-23 | 86-246 |
| *Thalamoporella* sp. | Indeterminate crab | Key *et al.* (2017) | Miocene | 504 | 14 | 31 | 365 |
| *Acanthodesia* sp. | Indeterminate leucosiid crab | Key *et al.* (2017) | Miocene | 43 | 6 | 11 | 96 |

benefit the bryozoan. Unfortunately, age of onset of sexual reproduction in bryozoan colonies is not often recorded in longitudinal studies due to the length of time required. Colony size at sexual maturity in encrusting cheilostome species ranges widely. For example, *Rallocytus ridiculs* reached sexual maturity at only four zooid size, many interstitial species reached sexual maturity by <10 zooids, *Drepanophora* sp. by 30 zooids, *Parasmittina* sp. and *Stylopoma spongites* by 150 zooids, but *Stylopoma* sp. not until it had 4600 zooids (Jackson and Wertheimer, 1985; Winston and Hakansson, 1986; Herrera *et al.* 1996; Grishenko *et al.* 2018). Applying the highest number to the encrusting colonies in Table 3, none ever reached sexual reproduction. Applying the lowest number, all reached sexual reproduction. Applying the mode (i.e., 150 days) most never reached the age of sexual reproduction. Unfortunately, most of the bryozoan species listed in Table 3 do not produce ovicells, which would have provided an independent test of female (though not male) sexual reproduction. For those colonies not reaching sexual maturity, the relationship with their host would be better described as commensalism. For those colonies that were estimated to have lived long enough to reach

sexual maturity (e.g., *Thalamoporella* sp. growing on an Eocene crab which lived up to 365 days), the relationship with their host was potentially mutualistic (Key and Schweitzer, 2019).

This study highlights the importance of publishing raw data tables, not just summary statistics or graphs, or at least including supplemental data tables or appendices. You never know how your data could be mined at a later date for another seemingly unrelated study.

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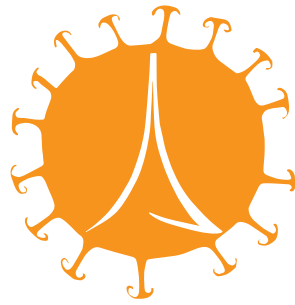
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