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ORIGINAL ARTICLE

Growth, production, and mortality of the chemosynthetic vesicomyid bivalve, *Calyptogena kilmeri* from cold seeps off central California

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Abstract

The vesicomyid *Calyptogena kilmeri* is one of the most abundant bivalves inhabiting chemosynthetic environments shallower than *c.* 1500 m along central California. We estimated the population size structure, biomass, rates of individual growth, somatic production, and mortality for *C. kilmeri*, based on sampling of seep habitats and tag–recapture studies at chemosynthetic communities in Monterey Bay, California. The composite growth rate of *C. kilmeri* over all sites was relatively high ($K = 0.25$), reaching *c.* 80% of asymptotic length (104.7 mm) in 6.6 years. The density of *C. kilmeri* was estimated as 938.5 ind. m^{-2} and biomass density varied from 704 to 2059 g ash free dry mass (AFDM) m^{-2}. Somatic production was also high (294–297 g·AFDM·m^{-2} ·year^{-1}), and production/biomass ratios for *C. kilmeri* varied from 0.14 to 0.42 among sites, related to variation in size–frequency distributions among sites. Instantaneous mortality rates estimated from size distributions ranged from 0.17 to 0.24 year^{-1}. Growth and somatic production by *C. kilmeri* are in the range reported for chemosynthetic bivalves from hydrothermal vent and seep habitats, as well as photosynthetic-based assemblages of inshore or intertidal bivalves, and greatly exceed rates reported for heterotrophic deep-sea benthos.

Problem

Bivalves in the family Vesicomyidae are common members of chemosynthetic communities inhabiting hydrothermal vent and seep habitats worldwide (Lutz & Kennish 1993; Sibuet & Olu 1998). All species known (>60) are nutritionally dependent upon sulfide-oxidizing bacterial endosymbionts housed in gill tissues. Most vesicomyids have been identified from seep environments, where they are a common dominant megafaunal taxon, particularly along the eastern and western Pacific margin.

The physiology and growth of chemosynthetic megafauna near hydrothermal vents were topics of early studies of hydrothermal vent biology, because of intense interest in the mode of life at vent systems. Growth by *Calyptogena magnifica*, a conspicuous vesicomyid at some vent sites, was estimated to be >4 cm year^{-1} at some locations (Turekian & Cochran 1981; Turekian *et al.* 1983). Growth by *C. magnifica* exceeded most shallow water bivalves and was far greater than heterotrophic deep-sea species (Lutz *et al.* 1988), indicative of the energy-rich character of vent environments (Lutz & Kennish 1993). Recent studies of growth by chemosynthetic mytilid mussels confirm the rapid, though variable growth of chemosynthetic bivalves, compared with non-chemosynthetic deep-sea groups (Nix *et al.* 1995; Smith *et al.* 2000; Bergquist *et al.* 2004).

Early studies of *C. magnifica* were the sole reports of growth for vesicomyids and it remains unclear whether *C. magnifica*, the largest extant vesicomyid (>22 cm maximum length), is typical of vesicomyids or chemosynthetic bivalves in general. Vesicomyids are considerably more diverse in seep environments than in either hydrothermal vents or whale-fall sites (Smith *et al.* 2003). Thus, their physiological performance could differ greatly from confamilial vent taxa.

Vesicomyids also dominate seep habitats along central California (Barry *et al.* 1996) with up to five species inhabiting individual seeps. *Calyptogena kilmeri* and *C. pacifica* are the dominant species for seeps shallower than *c.* 1500 m, and their distribution is coupled closely to the fluid chemistry of individual sites (Barry *et al.* 1997). *Calyptogena kilmeri* is the most abundant species in seeps with high sulfide concentrations (*i.e. c.* 1–6 mM HS^-) in the upper (0–10 cm) sediment column. *Calyptogena pacifica* is most common in locations with far lower sulfide levels (*c.* 0.1–0.5 mM HS^-), where *C. kilmeri* ranks second in abundance.

In this paper, we examine the individual growth rate of *C. kilmeri* based on tag–recapture studies. Coupling growth rates with estimates of size–mass relationships, faunal density, and population structure, we estimate biomass density, rates of somatic production, and mortality among seep locations.

Study area

Growth rate studies of *Calyptogena kilmeri* were measured at three seep locations in Monterey Bay, California. The sites, Clam Field, Clam Flat, and Mt Crushmore (Fig. 1) are inhabited principally by vesicomyid clams, and have been described in detail by Barry *et al.* (1996). All are located within the oxygen minimum zone, with oxygen tensions of bottom waters near 20 μM. Mt Crushmore (36.786 N, 122.042 W), located near 635 m depth along the steep, eroding walls of Monterey Canyon, is characterized by small patches of bivalves dominated by *C. pacifica* (73% of total vesicomyid abundance) but including *C. kilmeri* (12%), *C. packardana* (11%), and *C. stearnsii* (3%). Sulfide concentrations in the upper (5 cm) sediment column are low (0.1–0.6 mM HS^-), methane was not detected, and bottom water temperature is *c.* 5.3 °C. Clam Field (36.734 N, 122.002 W, 900 m, *c.* 4.3 °C) has higher sulfide (1–10 mM HS^-) and methane (5–50 μM CH_4) levels, with larger bivalve aggregations. *Calyptogena kilmeri* accounts for *c.* 85% of the vesicomyid assemblage at this site, which is inhabited by *C. pacifica*, *C. gigas*, *C. packardana*, and *C. stearnsii*. Clam Flat (36.745 N, 122.278 W, 1003 m) is located on a relatively flat region on the continental slope and has the highest sulfide (2–20 mM HS^-) and methane levels (*c.* 5–800 μM CH_4), and the lowest temperature (4.0 °C) among these sites. *Calyptogena kilmeri* is by far the dominant species, accounting for 99% of all individuals collected at the Clam Flat site.

The distribution of bivalves at all sites is patchy over small scales (*i.e.* 1–10 m), with dense aggregations (*c.* 0.5–2 m in size) of clams scattered among areas of locally high sulfide availability. Densities of clams are very high in aggregations, forming nearly 100% cover over the seabed, except in the center of some aggregations where high sulfide levels appear to exclude clams. Earlier studies by Barry *et al.* (1997) noted that sulfide was usually undetectable outside the margin of dense aggregations.

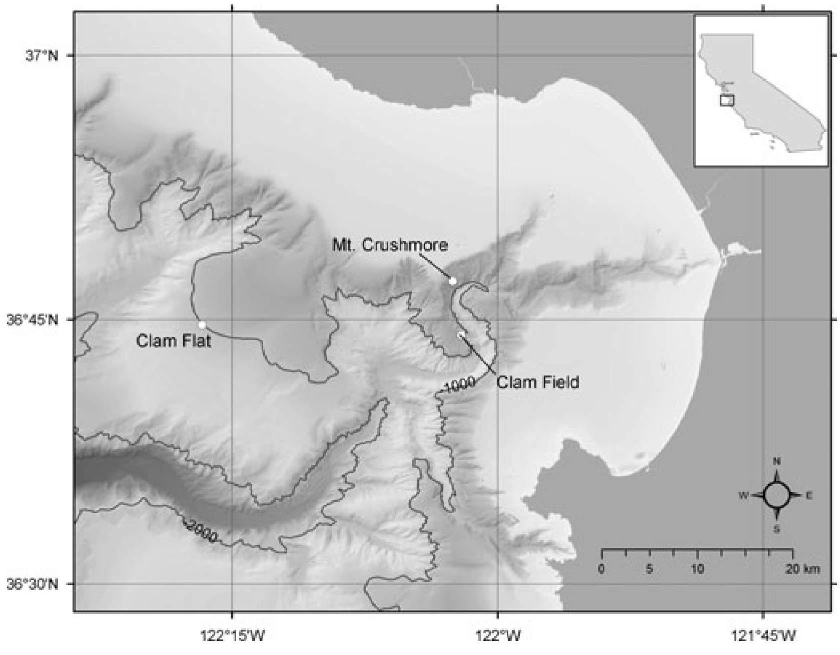

Fig. 1. Map of Monterey Bay indicating locations of chemosynthetic community sites utilized for size–frequency samples, growth, and productivity studies.

Material and Methods

Population size structure

The species composition and size structure of the vesicomyid assemblage at the three seep locations were sampled from 1992 to 2003. Collections of seep bivalves were made on nearly 100 dates by several investigators during this period. Most samples were non-quantitative, indiscriminate collections a number of individuals (10–100) using a scoop or suction sampler. In some but not all cases, sediment collected with the sample was sieved and small individuals were sorted, identified, and measured. Bivalves were identified and measured (maximum length, height, and width) to the nearest 0.1 mm. Measurements of total mass (shell + tissue) were taken for many individuals. Although these collections are a non-random sample of the vesicomyid assemblage, they are assumed to be roughly representative of the size structure of the populations of *C. kilmeri*. It is likely that smaller size classes were under-sampled by these methods, and are therefore under-represented in the estimated population structure.

Size distributions at each site (all years combined) were compared among sites using a Kolmogov–Smirnov (KS) test, based on the percent frequencies of individuals in each size bin (2-mm interval) of the total collected. Numerous small collections at each site were combined into yearly intervals to represent the time series of size distributions for *C. kilmeri* at each site.

To estimate the density (no. m^{-2}) of *C. kilmeri* within live bivalve aggregations at these sites, we collected a small number ($n = 3$) of quantitative samples from two seep sites. A box core device ($0.0206\ m^2$) was used to sample bivalve aggregations at the Clam Field and Clam Flat sites. In addition, the sediment community within a 25-cm diameter plastic ring inserted into a bivalve aggregation at the Clam Field site was collected using a suction sampler to collect animals and sediment within the ring to a depth of *c.* 15 cm. Vesicomyids from each of these three quantitative samples were identified, measured, and weighed. The average density of *C. kilmeri* determined from these collections was assumed to represent its typical abundance at these two sites. Although the sample size is limited, these samples targeted the densely populated aggregations of vesicomyids typically found in these seep communities. Seep habitats in this area have a generally sparse distribution of bivalve aggregations over scales of 5–100 m, but very high densities of bivalves within each aggregation (typically 0.5–2 m in scale). Quantitative samples of bivalve densities were not obtained from the Mt Crushmore site.

The abundance of *C. kilmeri* within each size class and site was estimated as the product of the proportional abundance within each size class (based on all available samples from each site) and the average density of *C. kilmeri* (938.5 ind. m^{-2}, SD = 652.6).

Tag–recapture studies

Rates of individual growth by *Calyptogena kilmeri* were measured using tag–recapture methods. *Calyptogena kilmeri* was collected from chemosynthetic communities at three sites reviewed above (Fig. 1) using the ROV *Ventana* operated by the Monterey Bay Aquarium Research Institute. Individuals were measured, marked with a numbered tag, and returned to a chemosynthetic community. In most cases, animals were returned to within 25 cm of the location collected.

During each tagging session, clams were collected from seeps using the ROV robotic arm and placed in a sample drawer. Before leaving the site, the location was marked (if clams were to be returned to the same location) with either a numbered stake inserted into the sediment, or by inserting a clam 'corral' (a 5-gallon plastic bucket with the bottom removed) into the sediment (*c.* 5 cm penetration) directly over the clam collection location (Fig. 2).

Measurement and tagging of *C. kilmeri* was performed aboard the *R/V Pt. Lobos*. Clams brought to the surface were placed in cold, hypoxic seawater to mimic conditions near the collection sites. Individuals were measured in triplicate to the nearest 0.1 mm along three shell axes (maximum length, maximum height, and maximum width), then marked with a numbered tag fixed with clear epoxy to the posterior end of one valve. Measurement and marking required *c.* 1–2 min of partial to full aerial exposure. Clams were held in the seawater bath until the following ROV dive (usually within 1–2 h) and returned to the seabed either unconfined (near a marked stake) or confined within a clam growth corral.

Subsets of clams were treated with fluorochromes to create a fluorescent growth zone in the shell to aid estimation of age and growth. The fluorochromes tetracycline or calcein were used to treat several lots of tagged vesicomyids. Tetracycline has been used successfully in aging studies for several taxa including bivalves (Dey & Bolton 1978; Pirker & Schiel 1993). Calcein has also been used in aging studies of various taxa (Day *et al.* 1995; Kaehler & McQuaid 1999; Ebert & Southon 2003; Marschal *et al.* 2004). Both can produce a fluorescent band in shells or other calcified structures and have been used with varying success. Bivalves labeled with tetracycline or calcein were injected with a dose of *c.* 50 mg tetracycline hydrochloride or calcein per kg wet body mass (mass estimated from size and size–mass relationships), similar to Monaghan (1993). Injections were performed during measurement and tagging activities. Clams labeled with fluorochromes were relocated to their site of collection,

Fig. 2. Photograph of clam growth corral, fabricated from 5-gallon bucket with the bottom removed. Growth corrals were used in many cases to prevent the dispersal of individuals during growth studies. Most bivalves visible are *Calyptogena kilmeri*.

Table 1. Summary of tag–recapture studies for *Calyptogena kilmeri* at three sites. The site, date deployed (T. date), number tagged, recovery date (R. date), number recovered (no. Rec.) (live:dead), and years at large are listed.

Site	T. Date	No. tagged	R. Date	No. Rec.	Years
Clam Field	4/5/1993	70	6/2/1993	1:0	0.16
			12/23/1993	30:7	0.72
			3/3/1995	7:1	1.91
			12/8/1998	1:1	5.68
Clam Field	12/23/1993	15	3/3/1995	7:0	1.19
Clam Field	5/12/1994	50	3/3/1995	1:0	0.81
Clam Flat	5/13/1993	23	1/1/1994	7:0	0.67
Mt Crushmore	8/13/1993	6	12/30/1993	1:0	0.38
Mt Crushmore	2/11/1994	61	3/17/1995	4:0	1.09

or in most cases, transplanted between seeps sites to evaluate changes in growth among sites.

Marked clams were recovered from 0.16 to 5.68 years following release (Table 1). Upon recovery, tagged clams were identified as live or dead by the flexure (if any) of foot or adductor muscles, then measured in triplicate as described above. Total mass (shell mass + tissue mass), shell mass, and tissue mass were measured for most individuals. Tissues were excised from the shell and frozen, and the valves, if applicable, were inspected using ultraviolet light.

Fluorochrome labeling of *C. kilmeri* was largely unsuccessful. Of 213 *C. kilmeri* labeled with fluorochromes, only five of 58 recaptured individuals (8%) were live upon recovery, compared with >80% live for untreated individuals. For a few fluorochrome-labeled individuals that survived, inspection under ultraviolet light (*c.* 500 nm) indicated that shell carbonate was deposited in the prismatic layer of the growth zone along the outer margin of the shell as well as throughout the exposed lamellar layer on the shell undersurface. Because of their high rates of mortality, no further analyses were performed for fluorochrome-labeled animals. In addition, because most animals transplanted between sites were labeled with a fluorochrome, we were unable to test the effects of translocation on the growth rate of *C. kilmeri*.

Estimation of individual growth rates

The growth rate of *Calyptogena kilmeri* was characterized using Fabens (1965) modification of von Bertalanffy's original growth function (von Bertalanffy 1938). The growth function,

$$S_2 = S_1 + (S_\infty - S_1)(1 - e^{-k(t_2 - t_1)}) \qquad (1)$$

[S_∞ = asymptotic length (mm); S_1 & S_2 = length at time 1 (t_1) & time 2 (t_2), respectively; k = the Brody growth coefficient] can be used with growth increment data over variable time periods, but assumes equal growth rates (k) for all individuals. Numerous authors (*e.g.* James 1991; Wang & Thomas 1995) have noted biases in growth parameter estimates using the Fabens method where growth rates are variable among individuals. Therefore, we also evaluated growth using (Wang 1998) modification of the Fabens method, which accounts for variation in individual growth, but found results very similar to the Fabens function.

Growth rates of *C. kilmeri* were compared among sites using an ANCOVA of growth *versus* site with initial size as the covariate. Because no significant variation among sites was detected (ANCOVA $F_{2,55} = 0.79$, n = 59, P > 0.46), data for all sites were combined for further analysis. Estimates of S_∞ and k for *C. kilmeri* over all sites were derived from an iterative non-linear regression of equation (1) using Systat (release 11) software and a Gauss–Newton, least squares estimation method.

A method similar to Natanson *et al.* (1999) was used to estimate age at $S = 0$ (t_0) as

$$t_0 = t + (1/k)[\ln((S_\infty - S_0)/S_\infty)]$$

S_0 was estimated to be 1.5 mm for *C. kilmeri* based on measurements of the smallest individuals observed in sieved samples of seep sediments.

Biomass and production

Population biomass and somatic production by *C. kilmeri* were estimated for the Clam Field and Clam Flat sites. Site-specific size–mass relationships and size–frequency distributions were combined with the overall growth rate [von Bertalanffy growth function (VBGF) parameters], and scaled by the overall mean faunal density (938.5 ind. m^{-2}, SD = 652.6) to estimate the size-specific distribution of biomass and production for *C. kilmeri* at each station.

Total mass and ash free dry mass (AFDM) were determined to the nearest 0.1 g for a subsample of *C. kilmeri* individuals from the Clam Field and Clam Flat sites. Dry mass was measured after tissues were dried to a stable weight (*c.* 48 h) at 60 °C. After combustion for 12 h at 550 °C, ash weight was measured and subtracted from the dry weight to determine AFDM. The relationship between maximum length (L) and AFDM, bivalve mass (M) was estimated by fitting coefficients A and B in a power function, $M = A(L)^B$. Size–mass relationships were compared among sites using ANCOVA (Systat), after checking for homogeneity of slopes [log(length) *versus* log(total mass) or log(AFDM)].

Biomass density ($g{\cdot}AFDM{\cdot}m^{-2}$) was calculated as $B = \sum N_i M_i$, over all size intervals, where N is the estimated density (no. m^{-2}) and M is the mean individual AFDM of size interval i.

The mass specific growth rate (G), was calculated as

$$G_i = Ck(S_\infty/S_i - 1)(y^{-1})$$

Coefficients k, and S_∞ approximate the VBGF parameters, C equals the exponent of the length to mass power function, and S_i is the mean length of size class i. Somatic production equals the summation over all size classes of the product of density (N), mass (M), and growth (G) or,

$$P = \sum N_i M_i G_i (\text{g AFDM m}^{-2}\text{year}^{-1})$$

A production (P)/biomass (B) ratio for *C. kilmeri* was calculated for the Clam Field and Clam Flat sites.

Mortality

Mortality rates for *C. kilmeri* at the Clam Field and Clam Flat sites were estimated from a length-converted catch curve (*sensu* Pauly & Calumpong 1984) for the composite of all available size–frequency collections for each site. Each size distribution was combined with VBGF parameters L_∞ and K (approximated by S_∞ and k) for each site to estimate the instantaneous rate of total mortality (Z), defined in a population growth model, $N_t = N_0 e^{-Zt}$, where N_0 and N_t are the abundance at the start and end of a period (*i.e.* year). The combination of samples over many months, seasons, and years is assumed to minimize the effect of recruitment pulses or inadequate sampling, and represent the stable age structure of the population. Thus, the decline in the right-hand side of the composite population age structure (calculated from the VBGF and size frequencies) provides an estimate of Z from

$$\ln(N_i/\Delta t_i) = a - Z \cdot t_i'$$

N_i equals the abundance of *C. kilmeri* in size class i, Δt_i is the time required for growth through size class i, and t_i is the relative age of size class i. Instantaneous mortality (Z) is the negative linear slope of a plot of $\ln(N_i/\Delta t_i)$ *versus* t_i. See Pauly & Calumpong (1984) for details.

Mortality was also estimated from the weighted average of annualized mortality rates for groups of tagged individuals defined by the period at liberty. Annualized rates were calculated as the proportional mortality of the group divided by the period (years) at large.

Results

Population size structure

Aggregate size–frequency distributions constructed from the composite of collections of *C. kilmeri* at each study site indicate a roughly bimodal population size distribution at the Clam Field and Mt Crushmore seeps, with an accumulation of larger, presumably older individuals (Fig. 3). No difference (KS = 0.21, $P < 0.10$) in size distributions was detected between the Clam Field and Mt Crushmore sites. The population structure at Clam Flat was dominated by small–medium size individuals, and differed from both the Clam Field (KS = 0.27, $P < 0.02$) and Mt Crushmore (KS = 0.26, $P < 0.03$) sites, likely due to the rarity of larger individuals.

The average density of *C. kilmeri* within dense clam aggregations at the Clam Field and Clam Flat sites, based on three quantitative samples, was 938.5 ind. m^{-2} (SD = 652.6). Visual estimates of the combined areal coverage of dense bivalve aggregations at each site based on ROV surveys were *c.* 250 m^{-2} (Clam Field) and *c.* 30 m^{-2} (Clam Flat).

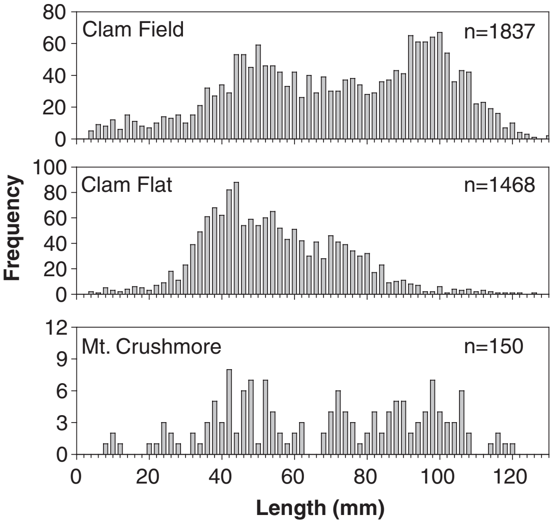

Fig. 3. Population size structure at Clam Field, Clam Flat, and Mt Crushmore seeps. Distributions represent the composite size structure from all collections at each site.

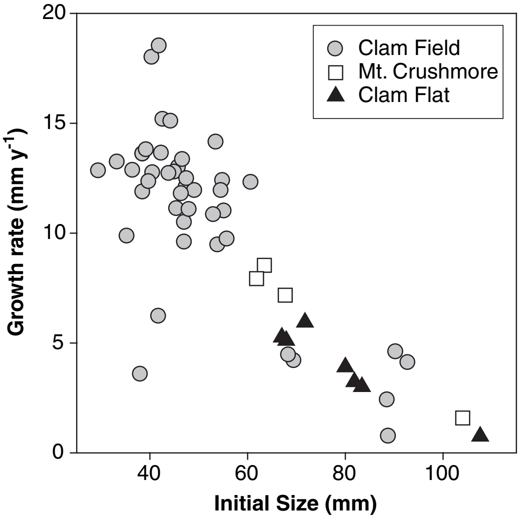

Fig. 4. Growth rate versus initial size for recaptured, tagged individuals of *Calyptogena kilmeri* at three sites.

Individual growth rates from tag–recapture studies

Fifty-nine of 225 tagged individuals of *C. kilmeri* released at the three sites were recovered live for use in VBGF analysis (Table 1). Because a large percentage of all tagged individuals were recovered from the Clam Field site, the sample size was much smaller for Clam Flat (n = 7) and Mt Crushmore (n = 5), reducing confidence in the estimation of growth rates for *C. kilmeri* at these sites. Non-linear regression of the combined samples from all sites (because of the non-significant site-related variation in annualized growth rates) indicated rapid growth by *C. kilmeri*, increasing in size by 10–20 mm year^{-1} at small sizes (Fig. 4), with diminishing growth as individuals approach asymptotic size [*i.e.* 80% of S_∞ (104.7 mm)] after 6.6 years, based on estimates of VBGF parameters (Fig. 5).

The VBGF derived from tag–recapture data exhibited a fairly close correspondence with the modal sizes in time series of size–frequency distributions characterizing populations of *C. kilmeri* at each site (Figs 6–8). The growth curve appeared to fit most closely changes in size modes for the Clam Field site. Growth curves also tracked modal sizes for the Clam Flat site, but were less clear for the Mt Crushmore site, where the sample size for *C. kilmeri* was small.

Length–mass relationships among stations

Length–mass relationships were generally similar among stations (Fig. 9), at least within overlapping size ranges.

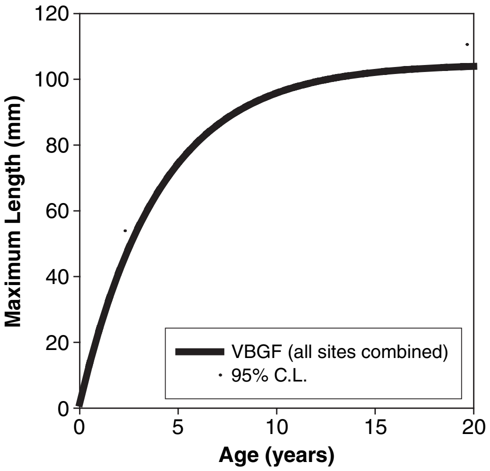

Fig. 5. Growth model (von Bertalanffy growth function (VBGF) for *Calyptogena kilmeri*. Bold black curve indicates the VBGF model ($S_t = S_\infty(1-e^{-k(t-t0)})$) for all sites combined, based on tag–recapture data, where S = length and t = age in years. Thinner dotted curves indicate the upper and lower 95% confidence limits around the regression. VBGF parameters [K (95% CI), S_∞ (95% CI), t_0, Res. SS, and r^2] for all sites are: [0.245 (0.04), 104.7 (6.31), −0.06, 321.3, 0.99].

However, the slopes of log(length) *versus* log(total mass) differed among stations ($F_{2,893} = 8.56$, $P < 0.001$), limiting comparisons of length-adjusted mass among stations. When comparisons of length-adjusted mass among stations were made using only individuals <75 mm in length, the slopes test was non-significant and no significant variation (ANCOVA) in intercepts were detected. Thus, the dominance of larger size classes at the Clam Field site and particularly the Mt Crushmore site appears

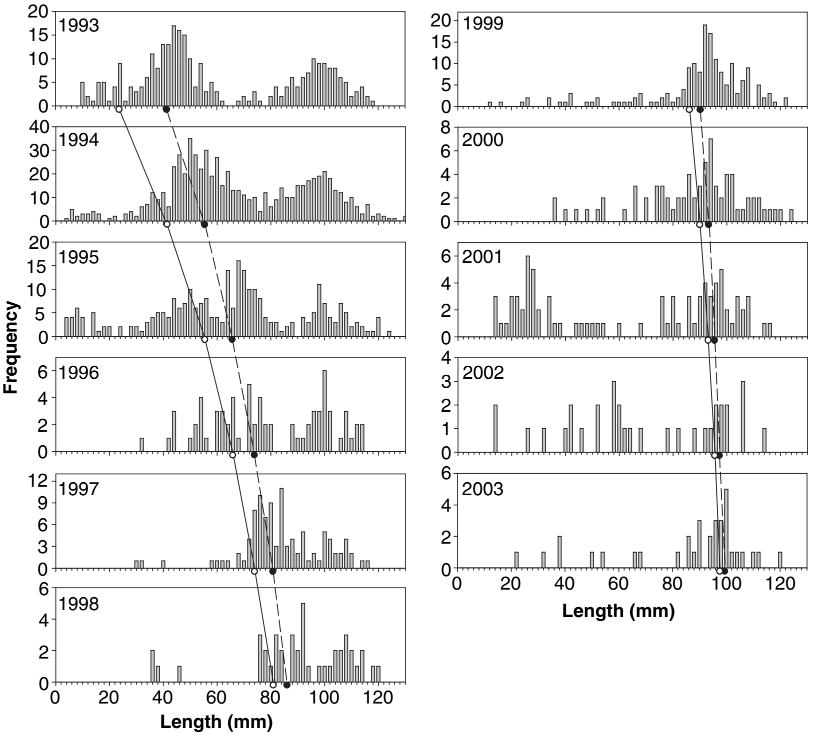

Fig. 6. Composite yearly size–frequency histograms for *Calyptogena kilmeri* at the Clam Field seep site. von Bertalanffy growth function curves from age 1 to 11 (open circles) and age 2 to 12 (filled circles) are superimposed on the size–frequency distributions to compare changes in modal sizes with growth rates expected from tagging studies.

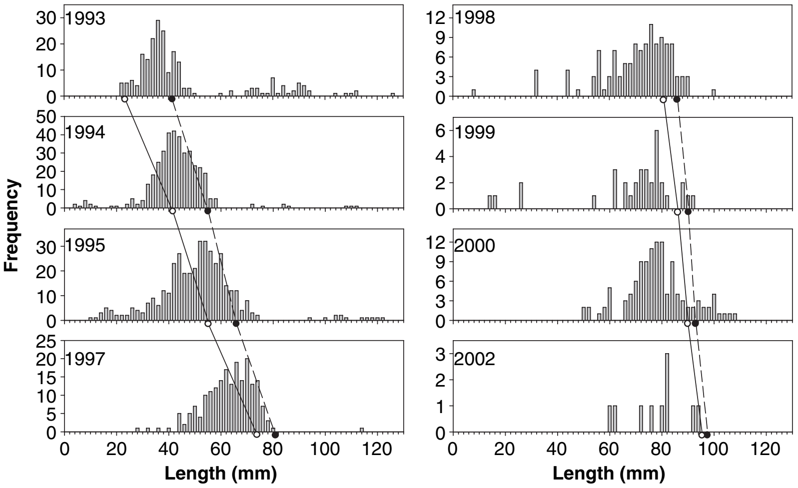

Fig. 7. Composite yearly size–frequency histograms for *Calyptogena kilmeri* at the Clam Flat seep site. von Bertalanffy growth function sizes (ages 1–10; open circles and age 2–11; closed circles) are superimposed on the size–frequency histograms as in Fig. 6.

to be responsible for the difference in size–mass relationships among locations.

Analysis of length *versus* AFDM revealed that length-adjusted AFDM was greater at the Clam Field site than at Clam Flat (ANCOVA, $F_{1,36} = 12.5$, $P < 0.01$). This result is likely also related to the larger average size of individuals analyzed from the Clam Field site (mean length = 92.8 mm, SD = 1.2) than the Clam Flat site (mean length = 72.7 mm, SD = 7.5; $t = 8.7$, df = 72, $P < 0.0001$; Fig. 3).

Population biomass and productivity

The biomass distribution at the Clam Field site differed significantly from Clam Flat (KS = 0.35, $P < 0.001$), with a much larger total population biomass (2059.3 g·AFDM·m^{-2}, SD = 1432.0) than at Clam Flat (704.6 g·AFDM·m^{-2}, SD = 489.9). This gap in biomass density between sites is again related to the greater abundance of large, high-biomass individuals at the Clam Field site (Fig. 10).

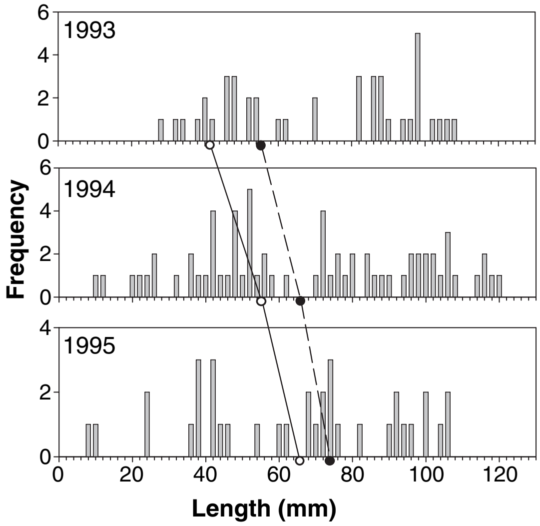

Fig. 8. Composite yearly size–frequency histograms for *Calyptogena kilmeri* at the Mt Crushmore seep site. von Bertalanffy growth function sizes (ages 3–5; open circles) and (age 4–6; closed circles) are superimposed on the size–frequency histograms as in Fig 6.

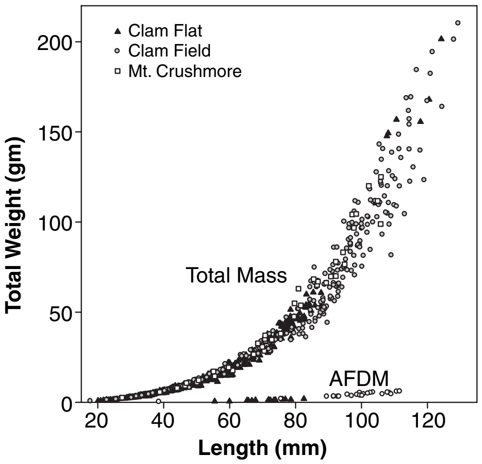

Fig. 9. Length–mass relationships for *Calyptogena kilmeri*. Total mass indicates total animal mass (shell + tissue). Ash free dry mass includes only tissue mass. Sites indicated by symbols. Length *versus* mass was modeled as mass M = A×Length^B. Parameters (A, B, r^2) for total mass *versus* length are: Clam Field [3.61×10^{-5}, 3.20, 0.96], Clam Flat [3.23×10^{-5}, 3.24, 0.99], Mt Crushmore [6.35×10^{-5}, 3.10, 0.97]. Parameters for AFDM *versus* length are: Clam Field [5.31×10^{-6}, 2.95, 0.87], Clam Flat [2.54×10^{-6}, 3.07, 0.91] (all relationships significant with $P < 0.001$).

Length-specific somatic tissue production for *C. kilmeri*, estimated by combining site-specific individual growth rates with length–mass relationships, differed slightly, but non-significantly between the Clam Field and Clam Flat sites (Fig. 11). Individual production peaked at both locations near *c.* 65–70% of asymptotic size.

Length-specific production, scaled by density in each size class (Fig. 10) shows the very similar potential for growth by *C. kilmeri* at the Clam Field and Clam Flat sites. The general absence of a mode of larger, older individuals at Clam Flat led to differences in biomass, but did not result in a lower total production (297 g·AFDM·m^{-2}·year^{-1}) than the Clam Field site (294 g·AFDM·m^{-2}·year^{-1}), as the majority of somatic production is from small to medium size classes. Had sufficient tag–recapture data been available from the Clam Flat site, differences in VBGF parameters might have increased the differences in production between sites. The smaller mean size of the population of *C. kilmeri* at the Clam Flat site resulted in a much higher overall production/biomass ratio (P/B = 0.42) compared with the Clam Field site (P/B = 0.14) where large, low-productivity individuals accounted for a large proportion of the biomass.

Mortality

Estimates of annual proportional mortality (Z) from relative age–frequency distributions varied among stations, with the highest mortality at the Clam Flat site (Z = 0.27 year^{-1}; Fig. 12). Annual mortality for the Clam Field (Z = 0.21 year^{-1}) and Mt Crushmore (Z = 0.18 year^{-1}) sites were lower because of the greater abundance of large, older, individuals. Rates for all stations were based on the decline in abundance of ages *c.* 2.5+ in the overall length distribution.

An independent estimate of the annual proportional mortality rate for *C. kilmeri*, estimated from ratios of dead/total tagged animals recaptured was 0.15 year^{-1}, resulting in an estimate of Z = 0.16.

Discussion

Population structure

Differences in the size distributions of *C. kilmeri* among seep sites are indicative of variation in demographic rates, individual growth rates, or both. The low abundance of large size classes at the Clam Flat site and bimodal character of sizes at Clam Field and Clam Flat suggest that the age structures of these populations are unstable, with episodic recruitment pulses which dominate size distributions producing peaks in juvenile or adult sizes. Alternatively, stable, bimodal size distributions may arise from changes in rates of growth or mortality with age (Barry & Tegner 1990). In addition, temporal changes in the habitability of seep environments related to sulfide availability may exert strong influence on the stability of vesicomyid populations.

The ratio of mortality-to-growth for *C. kilmeri* is low at all sites, suggesting that these populations are limited

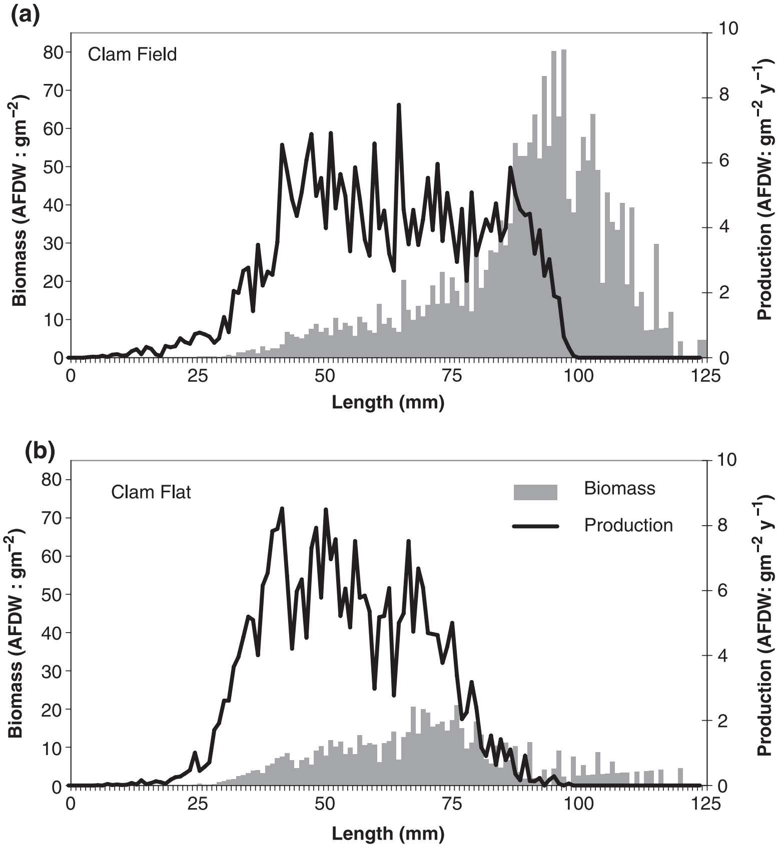

Fig. 10. Biomass density (g·AFDM·m^{-2}) and somatic production (g·AFDM·m^{-2}·year^{-1}) for *Calyptogena kilmeri* versus size (total length) by site. Biomass density (bars) is the total biomass per size interval, based on the size mass relationships determined for the site. Production at each site was calculated using growth parameters estimated from tag-recapture studies, and site-specific size–mass relationships. a: Clam Field. b: Clam Flat. Note the lower biomass, but similar somatic production at the Clam Flat site.

principally by recruitment and have low rates of mortality. An index of mortality to growth developed by Brey & Gage (1997) as $\Delta_{Z/K} = \log(Z_{\text{measured}}/Z_{\text{predicted}})$, where $\log(Z_{\text{predicted}} = 0.339 + 1.037(\log(K_{\text{measured}})))$, was negative for each site (Clam Field = −0.38; Clam Flat = −0.27, Mt Crushmore = −0.45; K = 0.245 for all sites). Negative values of $\Delta_{Z/K}$ are generally found in populations with a lower than average ratio of mortality-to-growth, while those with high mortality rates (*e.g.* heavily fished species) typically have positive $\Delta_{Z/K}$ indices (Brey & Gage 1997). Combined with size–frequency data from each site, the $\Delta_{Z/K}$ indices are consistent with population dynamics dominated by limited or variable recruitment rates or both, but generally low rates of mortality. Thus, predation rates may be quite low in these populations, even though they appear to be quite vulnerable to some predators (*e.g.* octopus, decapod crustaceans). Rates of predation may be influenced by several factors, including sulfidic sediments and tissues which may inhibit predators, or individual size. Predation may be the highest for small, thin-shelled juveniles, then decline as individuals grow to a larger size with thicker, stronger shells. It is not possible to discriminate between larval supply and early post-settlement survival as controls on recruitment rates.

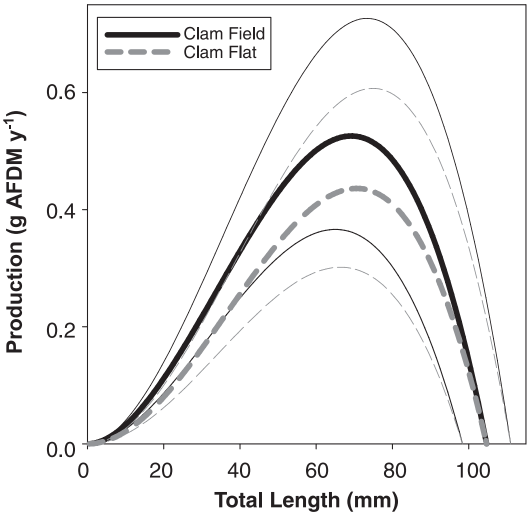

Fig. 11. Size-specific somatic production for *Calyptogena kilmeri* at seep sites in Monterey Bay. Each thick curve describes the annual production (g·AFDM·year^{-1}) by individual total length, based on the von Bertalanffy growth function parameters over all sites and the site-specific size: biomass relationships. Ninety-five percent confidence limits indicated by thin lines. Note the higher peak somatic production at the Clam Field site, which is related to its higher growth coefficient (K).

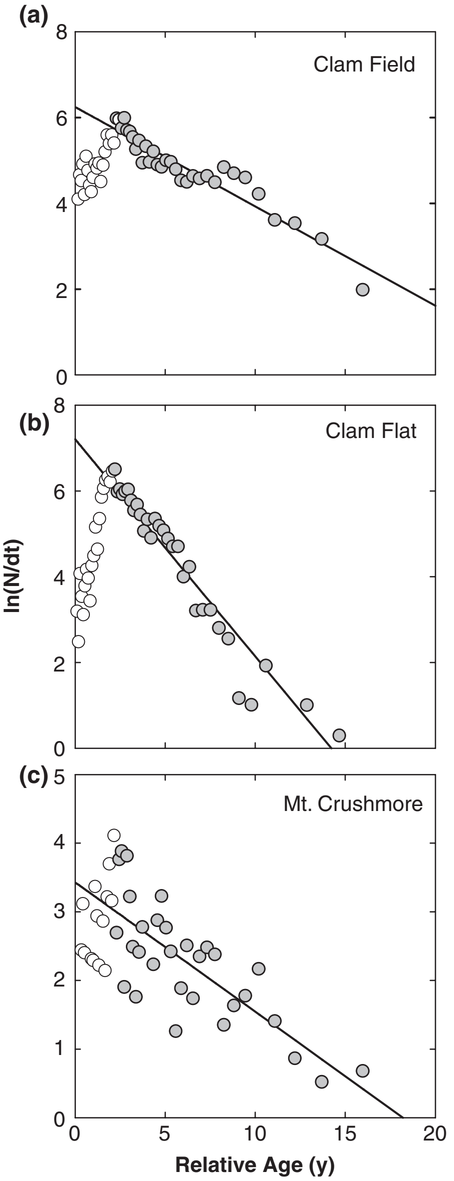

Fig. 12. Relative age–frequency distributions for *Calyptogena kilmeri* at seep sites in Monterey Bay. Gray symbols indicate data used to calculate the slope (–*Z*) of the linear regression. Mortality parameters Z (95% CI), n, r^2 are listed for each site. a: Clam Field [0.21 year^{-1} (0.03), 29, 0.94]. b: Clam Flat [0.27 year^{-1}, (0.03), 34, 0.96]. c: Mt Crushmore [0.18 year^{-1} (0.05), 35, 0.81].

Growth rate variability

Growth rates reported here for *C. kilmeri* are generally similar to those estimated for other bivalve taxa from cold seep and hydrothermal vent environments. Radionuclide dating techniques were used to estimate growth in *C. magnifica* at the Galapagos Spreading Center (Turekian & Cochran 1981) and the East Pacific Rise hydrothermal vents (Turekian *et al.* 1983). Lutz *et al.* (1988) also modeled growth of *C. magnifica* at these sites. Growth of *C. magnifica* varied 15-fold (2.7–40 mm·year^{-1}) between these sites, suggesting a large impact of site to site environmental variation (*i.e.* sulfide availability). In addition, the authors reported considerable variation in growth rate within individual clams, suggesting that both spatial and temporal variation in energy availability may modulate vesicomyid growth. Growth by chemosynthetic mytilids at Gulf of Mexico seeps, which are similar in size to *C. kilmeri*, varies considerably (*c.* −1 to 18 mm·year^{-1}) depending on the availability of methane and perhaps sulfide (Nix *et al.* 1995; Smith *et al.* 2000; Bergquist *et al.* 2004), with growth coefficients from K = 0.02 to 0.21. Although limited tag–recapture data prevented a full characterization of *C. kilmeri* growth at each site, the non-significant ANCOVA comparing growth among sites, and results of size–frequency analyses indicated fairly similar growth at all stations. Little information is available presently concerning variation in growth within individuals.

Growth by chemosynthetic taxa from vent and seep environments overlaps most closely with heterotrophic, shallow-water taxa found in some of the most productive ocean habitats. For example, growth rates of two shallow-water venerids similar in size to seep vesicomyids, *Callista chione* (K = 0.24; *c.* 15 mm·year^{-1}, $S_\infty = 93$ mm) from the Aegean Sea (Metaxatos 2004), and *Eurhomalea exalbida* (K = 0.15, $S_\infty = 74$ mm) from the shallow subtidal in Ushuaia Bay in the Beagle Channel (Lomovasky *et al.* 2002), both overlap the values typical for chemosynthetic bivalves.

In contrast, growth rates reported for most chemosynthetic metazoans including vesicomyids are far greater than non-chemosynthetic, deep-sea species, due presumably to the severe limitations on energy availability for bathyal and deeper taxa. Even though few estimates of growth rates and production are available, deep-sea bivalves are small and considered to be slow-growing (Allen 1979; Oliver & Allen 1980). The deep-sea clam *Tindaria callistiformis* from 3800 m depth in the North Atlantic reportedly requires 100+ years (SD = 38 years) to reach a maximum size near 8 mm (Turekian *et al.* 1975). Gage (1994) estimated much more rapid growth for the bathyal nuculanid *Ledella pustulosa* (*c.* 1 mm·year^{-1}), though it was still much lower than *C. kilmeri*. A sympatric species, *Yoldiella jeffreysi*, had size–frequency distributions similar to *L. pustulosa*, suggesting a similar pattern of growth. Thus, these nuculanoid protobranchs appear to grow to adult size in only a few years.

Production of seep/vent communities

Production by chemosynthetic assemblages at hydrothermal vent and cold seep habitats is expected to be higher than for heterotrophic, deep-sea benthos dependent upon organic input from surface waters. Reports of secondary production at bathyal depths support this idea. Production by a bivalve-dominated sediment community in the Rockall Trough (2900 m) was reported as *c.* 0.12 g wet weight $\text{m}^{-2}\cdot\text{year}^{-1}$ (Gage 1992). Gage (2003) also measured the productivity of a bathyal (700–1000 m) brittle star (*Ophiocten gracilis*) assemblage (*c.* 0.06 $\text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) off Scotland. Both rates were far lower than estimated in this study for *C. kilmeri* ($294\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}\cdot\text{year}^{-1} = 2{,}292\ \text{g}\cdot\text{wet wt.}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) aggregations, which are 4 orders of magnitude more productive than the Rockall Trough benthos, and 3 orders more than the slope ophiuroid assemblage. However, because *C. kilmeri* may dominate productivity in the seep community to a greater extent than *Ophiopectin* in the bathyal community, this comparison probably overestimates the ratio of seep to bathyal ophiuroid community production.

A more conservative estimate of the ratio of seep/non-seep production can be made by comparing production by *C. kilmeri* to Brey and Gerdes' (1998) characterization of shallow to abyssal macrobenthic productivity. Brey and Gerdes related production by macrobenthic communities to water depth as $\log(\text{production}) = 1.273–0.419(\text{depth} + 1)$. Using this relationship, the expected productivity by typical heterotrophic benthos at the average depth of the three seep study sites (846 m) is $1.1\ \text{gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1} =$ *c.* $2.4\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$, or >100 times lower than estimated for *C. kilmeri*. Alternatively, we can estimate heterotrophic benthic production from the sinking particulate flux (*c.* $14\ \text{gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$; Pilskaln *et al.* 1998) multiplied by the dynamic ecotrophic efficiency (e) estimated near 0.25 (Brey 2001), yielding a benthic productivity near $3.6\ \text{gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$, still only 1.5% of production estimated for *C. kilmeri*.

Although secondary production by seep vesicomyids is clearly high in the context of heterotrophic bathyal macrobenthos, it appears comparable to production in other seep and vent assemblages, based on the high rates of growth reported among chemosynthetic taxa, ranging from seep mytilids (Nix *et al.* 1995; Bergquist *et al.* 2004) to *Riftia* sp. from hydrothermal vents (Roux *et al.* 1989; Lutz *et al.* 1994). Production by very slow-growing vestimenterans (Fisher *et al.* 1997; Bergquist *et al.* 2000) is low, but may nonetheless exceed that of heterotrophic deep-sea communities.

Somatic production by vesicomyids is also generally higher than that of most heterotrophic, macroinvertebrate assemblages in marine benthic habitats. Cusson & Bourget's (2005a) review of benthic production focused principally on coastal (<50 m depth) environments and reported average ranges in productivity of $0.9–4.0\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ among major invertebrate taxa. Molluscan assemblages had the highest rates of production ($4.0\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$), but these average rates were still *c.* 60 times lower than estimated for *C. kilmeri*.

Intertidal bivalve communities along productive shores appear to have rates of production comparable with seep and vent communities. Somatic production in intertidal mussel communities is reported to be *c.* $640\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ (Cusson & Bourget 2005b), exceeding that of most nearshore benthos, but comparable with production by *C. kilmeri*. Production by surf clams (*Donax serra*) along South African shores ($167–637\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$; Laudien *et al.* 2003) is also similar to our estimates for a bathyal chemosynthetic vesicomyid. Although comparable in production, vesicomyid assemblages explored in Monterey Bay were far less extensive than these productive shallow water bivalve assemblages.

P/B ratios for *C. kilmeri* ($0.14–0.42\ \text{year}^{-1}$) were low compared with most non-chemosynthetic taxa surveyed (see Cusson & Bourget 2005a), including molluscs (P/B *c.* 1.77). However, this low P/B ratio is consistent with the global patterns identified by Cusson & Bourget (2005a), showing a negative correlation of P/B with life span and body mass, and positive relationship with biomass density. *Calyptogena kilmeri* has large body mass compared with typical marine bivalves, with a moderately high maximum age expected to be near 15–30 years, based on growth and mortality estimates. In addition, the biomass density of *C. kilmeri* (*c.* $705–2059\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}$) is far greater than the average molluscan taxon (*c.* $2.24\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}$; Cusson & Bourget 2005a). *Calyptogena kilmeri* biomass also exceeds the benthic biomass of all macrobenthic communities of comparable depth reported by Brey & Gerdes (1997), and is more similar to shallow-water mytilids ($773.7\ \text{g}\cdot\text{AFDM}\cdot\text{m}^{-2}$; Cusson & Bourget 2005b). Relatively low P/B ratios and high rates of production (apparently due to large body size) are probably typical of many densely aggregated chemosynthetic assemblages.

The population dynamics of *C. kilmeri* in Monterey Bay chemosynthetic assemblages appear to include relatively rapid rates of population turnover (*i.e.* replacement by death and recruitment), in contrast with initial observations of growth and succession in seep communities. Although rapid colonization, growth, and succession are typical for hydrothermal vent communities (Smith & Hessler 1987; Shank 1999), the growth rates and population dynamics of some of the first seep megafauna studied were slow, particularly seep vestimentiferans with very slow growth and low rates of mortality (*e.g. Lamellibrachia luymesi*; 0.02–0.12% per year) (Bergquist *et al.* 2000, 2003; Cordes *et al.* 2005). Vesicomyids, like many other chemosynthetic bivalves, are intermediate in the spectrum of growth and population replacement observed in hydrothermal vent and seep systems, with fairly high growth and mortality rates.

Olu *et al.* (1996) proposed that vesicomyids are initial colonists of sulfidic seep sediments off Barbados, later replaced by chemosynthetic mytilid mussels, although the successional mechanisms remain unclear. Because methanotrophic or sulfide-oxidizing mytilids have not been discovered in northeastern Pacific seep communities, likely due to limited methane availability near the seabed because of limited fluxes, rapid mixing, or both (Barry *et al.* 1997), successional pathways for seep communities in this area may be shorter than for seep environments drawing from a larger potential species pool. Succession may thus be controlled by geochemical limits on the availability of reduced inorganic compounds (*i.e.* sulfide & methane). Because local fluid chemistry may not support large vestimentiferan or mytilid populations, vesicomyids may be released from competition with these potentially effective late-successional taxa. Progress in understanding the physiology, growth, and production of chemosynthetic species has been rapid during the past two decades. Complementary studies of chemosynthetic taxa will broaden the demographic context of these studies to include processes influencing reproduction, colonization, and recruitment, enabling a more comprehensive perspective concerning the development and regulation of chemosynthetic communities.

Summary

Calyptogena kilmeri, a dominant bivalve inhabiting chemosynthetic communities shallower than 1500 m in Monterey Bay, California, has rates of individual growth and somatic production comparable with fast-growing mytilid mussels at methane seeps and coastal or intertidal bivalves. The range in growth rates estimated from tag–recapture studies indicates growth to 80% of asymptotic size in *c.* 6.6 years. Somatic production for *C. kilmeri* is 2–4 orders of magnitude greater than reported for non-chemosynthetic, deep-sea communities. These results support the notion that vesicomyid clams inhabiting chemosynthetic environments in the deep sea have rates of growth and production similar to productive nearshore assemblages and differ greatly from more typical, heterotrophic deep-sea taxa.

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