

The paradox of *Metridia* spp. egg production rates: a new technique and measurements from the coastal Gulf of Alaska

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ABSTRACT: Egg production rates of the copepods *Metridia pacifica* and *M. okhotensis* were examined in the Gulf of Alaska over an annual cycle using a new incubation system that separates females from their eggs and keeps the eggs undisturbed prior to observation. *Metridia* spp. eggs frequently break-down during incubation, leading to severe underestimates of egg production by traditional methods. Egg production by *M. pacifica* continued throughout most of the year, while that of *M. okhotensis* was confined to the spring. Egg production rates of *M. pacifica* peaked in May at 30 eggs female⁻¹ d⁻¹ and averaged 16 eggs female⁻¹ d⁻¹ from March through October. Egg production of *M. okhotensis* was limited to spring and averaged 28 eggs female⁻¹ d⁻¹ during April and May. Equivalent specific egg production rates for the 2 species over these periods averaged 10 and 11%, respectively, comparable to other calanoid species from this region. For *M. pacifica*, most of the variability in egg production rates could be attributed to ambient chlorophyll concentrations, after adjusting for the influence of temperature, with food-saturated specific egg production at 5°C equivalent to 17 to 18% of their body weight d⁻¹, and half saturation occurring at 1 to 1.5 mg chlorophyll a m⁻³.

KEY WORDS: Egg production · *Metridia pacifica* · *Metridia okhotensis* · Alaska · Techniques

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INTRODUCTION

Although plankton ecologists have been preoccupied with the biology of copepods for nearly a century, this effort has concentrated on only a handful of species that are either primarily coastal, or members of the family Calanidae (see Mauchline 1998). *Metridia* is among these neglected calanoid genera, and is often poorly represented in collections because it undergoes a strong diel migration (e.g. Batchelder 1985, Hirakawa & Imamura 1993). *Metridia* species occur throughout the world's oceans in temperate through sub-polar waters (Brodsky 1967), being among the more common medium- to large-bodied copepods in many regions (e.g. Smith & Vidal 1986, McLaren et al. 1989, Huntley & Escritor 1992, Incze et al. 1997, Sherman et al. 1998, Rebstock 2001, Hopcroft et al. 2002).

Throughout the North Pacific, *Metridia pacifica* is the most common species within the genus (Brodsky

1967), but the larger *M. okhotensis* is also relatively common, especially in deep, semi-enclosed systems such as the Okhotsk Sea (Brodsky 1967, 1977, Shebanova 1997), the deep Bering Sea (Ozaki et al. 2001), and fjords in the north-eastern Pacific (Gardner & Szabo 1982), including Alaskan coastal embayments (Coyle et al. 1990, Cooney et al. 2001). In the Gulf of Alaska, where sampling has been conducted consistently during night-time, *Metridia* species rank second in larger-bodied copepod abundance after *Neocalanus* species during spring and early summer, but typically rank first for the remainder of the year (Coyle & Pinchuk 2003).

To be such a prominent species, one would expect *Metridia* to have egg production rates comparable to other dominant broadcast spawning species. Paradoxically, the measured rates of egg production for *M. pacifica* have been consistently low (e.g. Batchelder & Miller 1989, Hirakawa & Imamura 1993). Preliminary

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incubations of *Metridia* species in the Gulf of Alaska suggested similarly low egg production; yet it was also observed that eggs laid in multi-well plates had usually disappeared by subsequent inspections. Egg cannibalism was implicated, so egg production 'towers' were designed that employed Nitex screens to separate the females from any eggs that they laid. Unlike most anti-cannibalism systems, these towers could be dismantled allowing observation of the eggs without disturbance. Here we report the rates and seasonal cycles of egg production for both *M. pacifica* and *M. okhotensis* species using these techniques.

MATERIALS AND METHODS

The study area in the northern Gulf of Alaska is part of the US Northeast Pacific GLOBEC program (see Weingartner et al. 2002). The region is characterized by a shelf of 100 to 300 m depth, with complex bathymetry and many deep-water coastal fjords and embayments (Fig. 1). In 2002, 7 cruises were conducted in March, April, May, July, August, October and December. Egg production work was executed at 4 stations distributed along the Seward line from inshore to just past the shelf break (i.e. Gak1, 4, 9, 13), plus 1 station along the western inner passage of Prince William Sound (PWS2) where the depth is 500 to 800 m. Water samples at these stations were collected by Niskin bottles for fluorometric estimation of chlorophyll *a* con-

centration and averaged over the upper 40 m of the water column (D. A. Stockwell & T. E. Whittedge unpubl. data).

Abundances of *Metridia* spp. females were determined from night-time collections employing a 1 m² MOCNESS fitted with 505 µm mesh nets fishing the upper 100 m at 1 m s⁻¹ in five 20 m strata (see Coyle & Pinchuk 2003). All females for egg production experiments were taken from an additional 100 µm mesh net equipped with non-filtering cod-ends fished in the upper 50 m for several minutes at less than 1 m s⁻¹. Samples were diluted immediately with ambient seawater, sorted within 0.5 to 2 h, and placed individually in 50 ml polycarbonate towers inserted into polystyrene 6 well tissue culture plates. Silicone O-rings provided a water-tight seal between the towers and plate wells. The bottom of the towers were fitted with 200 µm (for *M. pacifica*), or 400 µm (for *M. okhotensis*) Nitex mesh that was held ~0.5 cm above the bottom of the plate. Incubations of 48 active females per species were maintained at constant near ambient sea-surface temperature under natural lighting cycles. Incubations were terminated in the morning after 1 to 1.5 d of incubation. Water was removed from the towers with a large pipette fitted with 30 µm mesh over the tip. The position of the pipette tip was constantly adjusted to keep it immediately below the water's surface to minimize disturbance of deeper layers. When ~1 cm of water remained, the tower was removed from the plate, and the female backwashed off the mesh. This procedure rarely disturbed the eggs in the bottom of the multi-well.

Metridia spp. eggs were counted in their original positions within 1 to 2 h after dismantling the towers. Eggs were usually found in single, distinct clusters. Clutches laid on successive evenings could be distinguished not only by their spatial location, but also by noting the phase of embryonic development. Eggs were further distinguished as developing normally, infertile, or as having compromised development. As secondary production is defined as the 'elaboration of tissue, regardless of its fate' (Downing & Rigler 1984), we include all these eggs types in our estimates. This assumption would clearly overestimate the values appropriate for population fecundity models if abnormal development is reflective of that *in situ*, rather than a consequence of handling and techniques. During 2 cruises, side-by-side comparisons of this method were made to mutli-well plates without towers

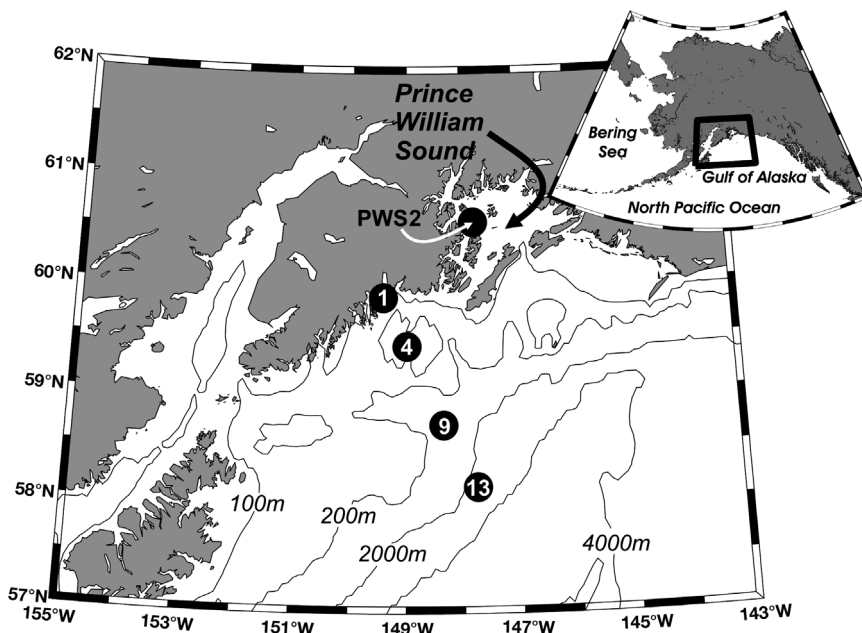


Fig. 1. Study area in the Gulf of Alaska. Four sites along the Seward line (Gak1, 4, 9, 13) plus the northern-most station in Prince William Sound (PWS2) were utilized for egg production experiments

installed (volume ~10 ml), and the more traditional methods of placing individual females in 250 ml bottles, or groups of 4 females in 1000 ml tissue culture flasks (Runge & Roff 2000). For the bottles and flasks, females and eggs were concentrated onto a 35 μm mesh at the termination of the experiment.

Individual females and eggs were then preserved for later measurement using a computer-assisted system (Roff & Hopcroft 1986). Female weights were predicted from a length–dry weight equation obtained using a mixture of females from both species at times when females were rich in lipids: $\log \text{DW} = -8.459 + 3.203 \log \text{PL}$ ($r^2 = 0.95$, $n = 16$), where DW is dry weight (μg) and PL is prosome length (μm). Female dry weights were determined to $\pm 0.1 \mu\text{g}$ using a Cahn Microbalance on pre-weighted pans, after drying at 55°C for 24 h. Egg weight was predicted from egg diameter, assuming a density of 0.14 $\text{ng C } \mu\text{m}^{-3}$ (Kjørboe & Sabatini 1994). Egg carbon was converted to ash-free dry weight (AFDW) assuming carbon as 40% of AFDW, and AFDW was assumed to be 90% of dry weight (Hirst & Bunker 2003). Linear regressions and curve fitting were carried out using SigmaPlot V8.0.

RESULTS

Although absolute abundances fluctuated between stations and over time, *Metridia pacifica* females could be found in surface waters at all stations throughout the year (Fig. 2), but were rare in December. In contrast, *M. okhotensis* was only found reliably inside Prince William Sound, and less reliably at Gak1, which is downstream in the Alaska Coastal Current that flows through the Sound. Female *M. okhotensis* became uncommon in surface waters after May once this layer warmed, although females were observed all year-round in deeper waters of the Sound.

Chlorophyll *a* peaked in April within the Sound and at Gak1, reaching values as high as 14 mg m^{-3} , but was

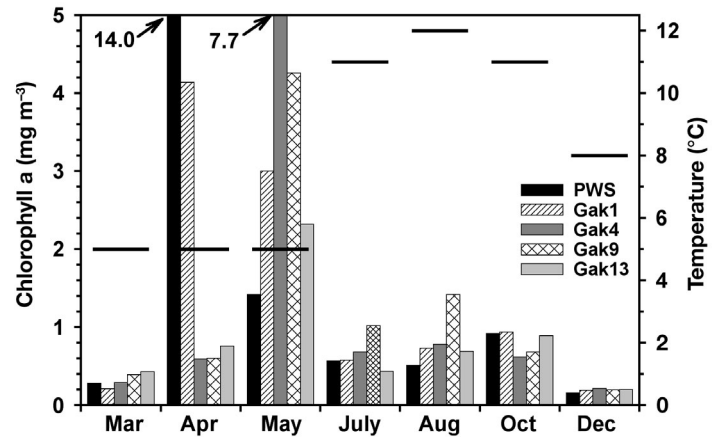


Fig. 3. Chlorophyll *a* concentration at experimental sites in the Gulf of Alaska during 2002 averaged over the upper 40 m. Incubation temperatures, indicated by horizontal lines, were set to reflect the temperature of the upper mixed layer. PWS: Prince William Sound

delayed until May in more offshore waters (Fig. 3). Mixed layer water temperature was typically ~5°C from March to May, and increased to over 14°C within Prince William Sound during July and August. Nonetheless, to reflect the temperatures more typical of the main sampling line, incubator temperatures during summer were limited to 12°C (Fig. 3).

Varying prevalence of the different egg types was observed. In March, none of the eggs laid appeared to develop normally (Fig. 4), and although this improved in April and May, it was generally less than 50% for *Metridia pacifica*. In contrast, most *M. pacifica* eggs laid in July, August and October developed normally; the single clutch laid in December failed to develop. Averaged over all experiments, 49% of *M. pacifica* eggs did not develop normally. *M. okhotensis* had a slightly different pattern, with a higher percentage of normally developing eggs in April and May. The abnormal egg category consisted primarily of eggs with either an absent or compromised membrane that

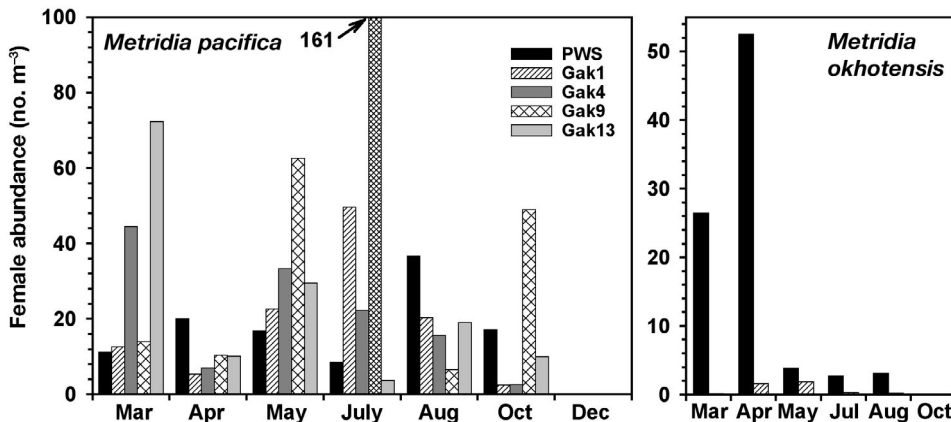


Fig. 2. *Metridia pacifica* and *M. okhotensis*. Abundance of females in the Gulf of Alaska during 2002. *M. okhotensis* was undetected at Gak4, 9 and 13 in all samples. MOCNESS samples are not available for the December cruise. PWS: Prince William Sound

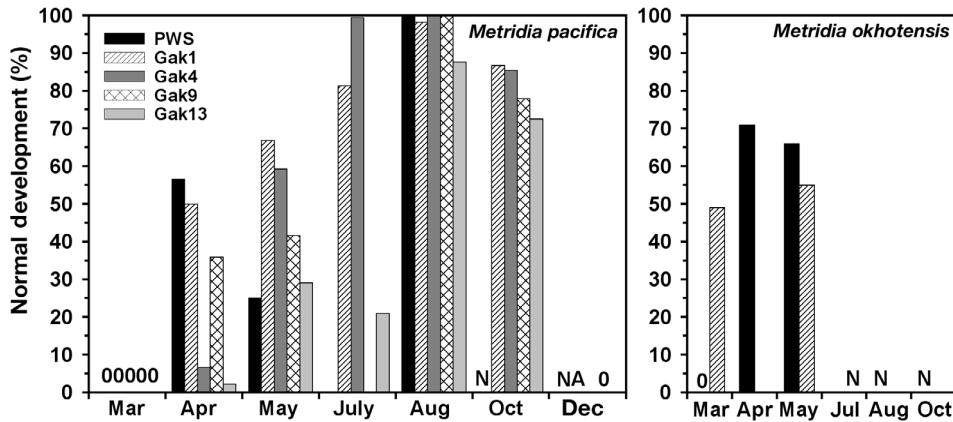


Fig. 4. *Metridia pacifica* and *M. okhotensis*. Percentage of eggs undergoing normal development during incubations in the Gulf of Alaska during 2002. Missing bars: no experiment; 0: females produced no normal eggs; N: no eggs were produced; A: females were absent from the collection site

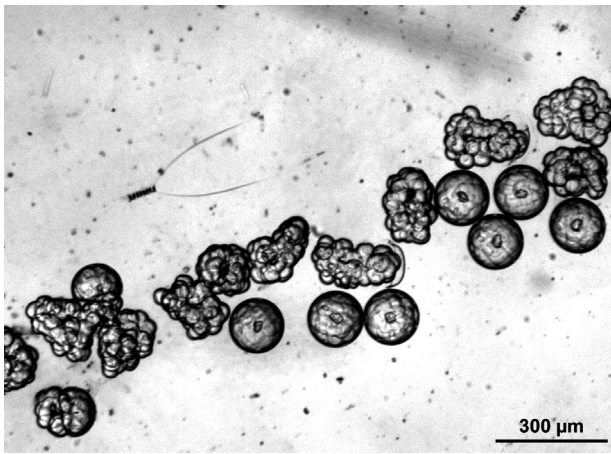


Fig. 5. *Metridia pacifica*. The 2 most commonly observed egg states: eggs undergoing normal development, and eggs that have lost their membrane and cellular cohesion. Both are at ~32 cell stage of embryonic development in this example

continued to divide eventually forming unorganized piles of undifferentiated cells (Fig. 5). Infertile eggs, that maintained their integrity but never divided, were relatively rare, seldom being more than 2 or 3 per clutch. Egg-sized spheres, that lacked a membrane, never divided, began to disintegrate rapidly, and were slightly more common in recently laid clutches; their numbers are likely underestimated.

Based on both direct observations during experimental set-up, and the observed stage of embryonic development during experimental break-down, most eggs appeared to be laid just before dawn (~04:00 to 06:00 h depending on the time of year). Females in experiments set up in the first half of the night were often found with 2 clutches of similar number but with a vastly different developmental stage. In contrast, females in experiments set-up near or after dawn, typically had only 1 clutch. Successive night clutches were less common in March, and most common in May.

When experiments were set up near or after dawn, egg production on the first night was consistently low and discounted. When few clutches were laid on the second night (as happened consistently in July and August), we considered only those clutches laid on the first night. Not surprisingly, abnormalities were more obvious in older clutches; therefore, our methods likely underestimate the true percentage of abnormal eggs for the most recent night's clutches. No attempt was made to establish the hatching success of normally developing eggs; however, in July and August, when incubation temperature was highest, experimental duration frequently approached hatching time, and high rates of hatching success were noted.

Females of both species were often observed with large lipid stores. Prosome length of females showed considerable seasonal variation in *Metridia pacifica*, with minimums in March (1600 to 1700 μm) and maximums in May (1950 to 2200 μm), and were relatively constant for the remainder of the year (~1700 to 1800 μm). Some inter-station differences occurred within the sampling period, but there was no consistent station differences over the annual cycle (Fig. 6). In contrast, *M. okhotensis* showed no seasonal variation in prosome length, remaining at ~2600 μm . Average clutch size tracked prosome length in *M. pacifica* (Fig. 6), but showed more pronounced seasonal variation. Considering all stations, average clutch size appeared to be lowest in March (~12 eggs), greatest in May (~49 eggs), and relatively similar across most other months, with no systematic patterns across stations (although notably, egg production shut down in Prince William Sound during October). The December data is less extensive than other months, and with the exception of a single female, no eggs were produced. Maximum clutch size produced by an individual *M. pacifica* was 103 eggs in May, with several females producing clutches of similar magnitude. Mean egg diameter in *M. pacifica* ranged from 140 to 150 μm . *M. okhotensis* produced larger clutches than *M. pacifica* (i.e. up to a

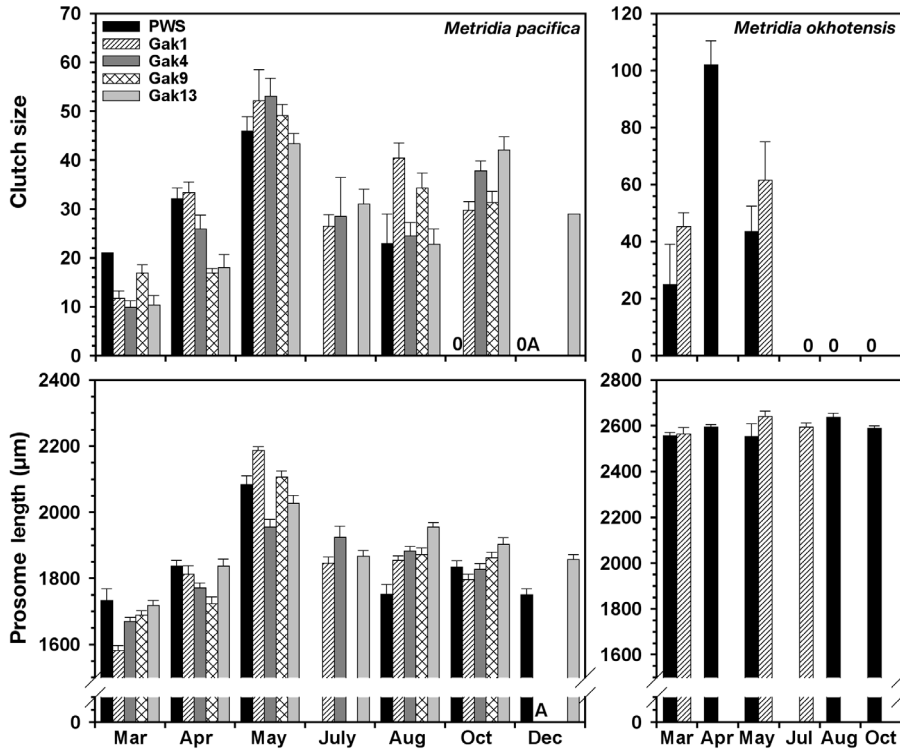


Fig. 6. *Metridia pacifica* and *M. okhotensis*. Egg clutch size and prosome length of females in the Gulf of Alaska during 2002. Standard errors of means indicated. 0: females produced no normal eggs; A: females were absent from the collection site

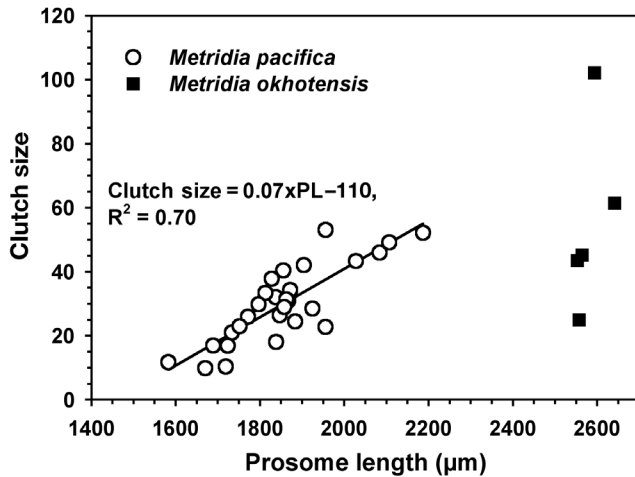


Fig. 7. *Metridia pacifica* and *M. okhotensis*. Relationship between size of the females of the 2 species (as prosome length) and the average number of eggs in the clutches produced for each experiment. Experiments where no clutches were produced have been excluded

maximum of 148 eggs by an individual) and larger eggs (170 to 180 μm diameter), but unlike *M. pacifica*, egg laying was restricted to March through May. Average clutch size was related to female prosome length in *M. pacifica* ($r^2 = 0.63$), but not in *M. okhotensis* (Fig. 7).

Accounting for the females that did not produce eggs, *Metridia pacifica* populations averaged 16 eggs female⁻¹ d⁻¹ from March through October (Fig. 8), with egg production rates (EPRs) consistently lower in March (average 3 eggs female⁻¹ d⁻¹), and generally highest in May (average 30 eggs female⁻¹ d⁻¹). *M. okhotensis* populations averaged 28 eggs female⁻¹ d⁻¹ in April and May, had limited egg release in March, and produced no eggs during summer and fall. The *M. pacifica* females that produced clutches typically released the equivalent of 10 to 20% of their body weight as eggs (Fig. 9), with lower values in March, and consistently higher values in May. *M. okhotensis* that produced clutches typically released the equivalent of 25% of their body weight as eggs in April and May. Accounting for those females that did not release eggs, specific egg production (SEP) for the population of *M. pacifica* was only 1 to 4% in March, negligible

in December, but averaged 10% in the other months. The SEP seasonal pattern appears to be more stable than that observed for clutch size or EPR, as a higher percentage of females produced clutches during summer and fall than during spring, and because SEP accounts for seasonal changes in female body size. SEP for the population of *M. okhotensis* mirrored its EPR, averaging 11% over April and May.

Much of the observed patterns between stations could be attributed to ambient chlorophyll concentrations, after adjusting for temperature (Fig. 10) by a Q_{10} of 2.7 determined for food-saturated broadcasting adult copepods (Hirst & Bunker 2003). Curves fit to Michaelis-Menten form (lower curves) described a large part of the variation (adjusted r^2 of 0.59 or 0.69 dependent on the inclusion of the strongest outlying value: May, Gak1, lowest point). The data envelope was even better described by sigmoidal functions (Table 1), after removal of the 4 low out-lying values: both Chapman and Hill equations described similar levels of variation (adjusted r^2 of ~ 0.84) and although all 3 fitted parameters were significant for both of these curves, they were most significant for the Hill equation. All equations are consistent in indicating that food-saturated rates at 5°C result in 17 to 18% of their body weight going into egg production each day,

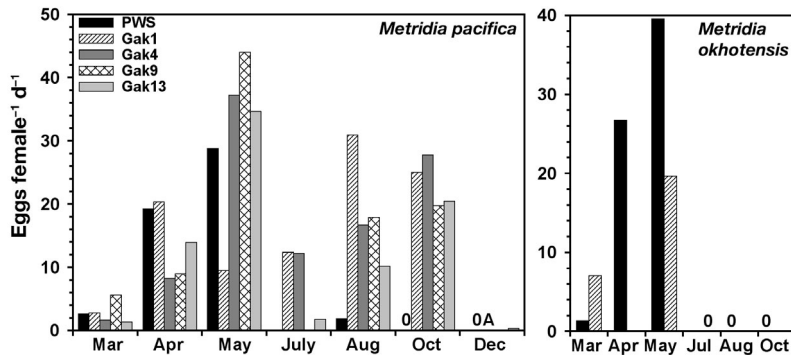


Fig. 8. *Metridia pacifica* and *M. okhotensis*. Egg production rate for the populations of females incubated in the Gulf of Alaska during 2002. Missing bars: no experiment; 0: females produced no clutches; A: females were absent from the collection site

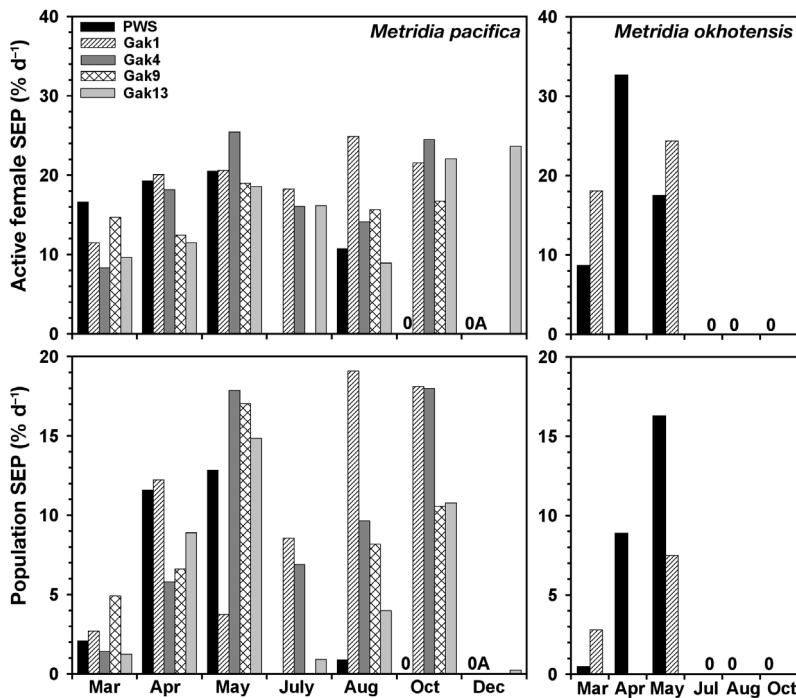


Fig. 9. *Metridia pacifica* and *M. okhotensis*. Specific egg production (SEP) of only those females producing eggs, and for the populations of females incubated in the Gulf of Alaska during 2002. Missing bars: no experiment; 0: females produced no clutches; A: females were absent from the collection site

with half saturation occurring at 1 to 1.5 mg chlorophyll $a\ m^{-3}$.

Results from side-by-side methodological comparisons emphasize the magnitude of error that could be associated with more traditional egg production methodology (Table 2). When using multi-wells or bottles, estimates of EPR were one-third to one-tenth of those obtained using the towers. Within a given contrast, all alternate methods appeared to yield similar results and gave the impression that most of the eggs were undergoing normal develop-

ment, when in fact, significant numbers of eggs were developing abnormally. Empty and/or damaged egg-cases were only rarely found. This suggests abnormal eggs are most likely dispersed by activity of the females, and not cannibalism of eggs per se. Initial trials using multi-wells alone, were similarly low, and frequently gave the impression that no egg production was occurring (Table 2).

DISCUSSION

In the Gulf of Alaska, *Metridia* species appear to undergo cycles of egg production related to annual cycles of phytoplankton biomass and temperature that are typical for most copepods (e.g. J. M. Napp unpubl. data, R. R. Hopcroft unpubl. data). The 2 species differ in that multiple generations of *M. pacifica* occur annually in the Gulf of Alaska, while only 1 generation occurs for *M. okhotensis*. Sampling was not conducted frequently enough to conclusively determine whether 2 (Hirakawa & Imamura 1993, Padmavati et al. 2004) or 3 (Batchelder 1985) generations per year occur for *M. pacifica* in the study area; however, based on the sustained reproductive activity, patterns of female abundance, and knowledge of temperature-dependent growth in the laboratory (Padmavati & Ikeda 2002), 3 are most likely. Similar to observations made for *M. lucens* (McLaren et al. 1989), over-wintering females are small compared to other generations, and those females completing development during the spring bloom are largest. In contrast, results from this study are more consistent with a single year life cycle for *M. okhotensis*, rather than a 2 y life cycle proposed for this species at slightly colder temperatures (Padmavati et al. 2004).

The daily specific rates of egg production for both species are consistent with those expected for copepods of these sizes, at these temperatures (Hirst & Lampitt 1998, Hirst & Bunker 2003). Rates of *Metridia* specific egg production are also comparable to those of other calanoid species in the Gulf of Alaska that have been simultaneously determined (J. M. Napp unpubl. data, R. R. Hopcroft unpubl. data). This is in sharp con-

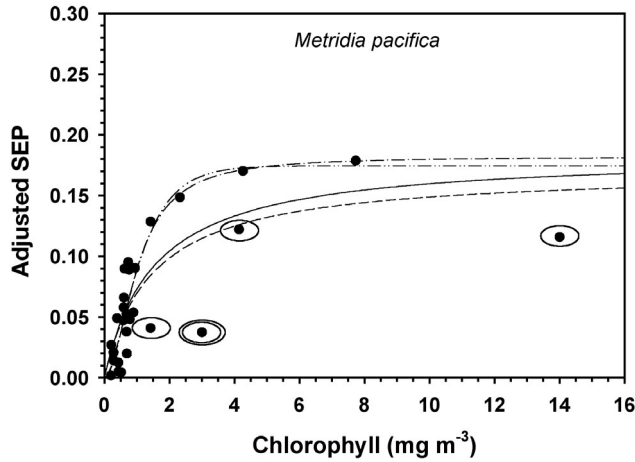


Fig. 10. *Metridia pacifica*. Functional relationship between population specific egg production (SEP) and chlorophyll *a* concentration. All data corrected to 5°C using a Q_{10} of 2.7. Curves fit to Michaelis-Menten form using all data (----) or after removal of the strongest outlying value (—) that occurred in May at Gak1 (point double circled). Sigmoidal Chapman (— · —) and Hill (····) functions fit after removal of the 4 low out-lying values (circled)

trast to the only 2 rates of egg production determined for *M. pacifica*: 6 eggs female⁻¹ d⁻¹ (Batchelder & Miller 1989) determined at Ocean Station P and off the Oregon Coast and 0.2 to 5.6 eggs female⁻¹ d⁻¹ in Toyama Bay, Japan (Hirakawa & Imamura 1993). In fact, all the published rates for the species within this genus are low: *M. lucens* ranges from 0 to 3.4 eggs female⁻¹ d⁻¹ at 5 to 7°C (Nielsen & Richardson 1989, Hay et al. 1991) and 2.1 ± 0.9 at 9 to 23°C (Richardson et al. 2001); *M. longa* ranges from 0.2 to 8.3 eggs female⁻¹ d⁻¹ at 1.5 to 2.5°C (Buskey & Sterns 1991, Hansen et al. 1996); *M. gerlachei* ranges from 0 to 6.2 eggs female⁻¹ d⁻¹ at 0 to 4°C (summarized in Schnack-Schiel 2001). All of these estimates have been obtained by harvesting the eggs with screens, and most by incubating groups of females. Maximum individual clutch size has only been reported in 2 cases: *M. gerlachei*, 42 eggs (Schnack-Schiel 2001), and *M. lucens*, 28 eggs (Richardson et al. 2001). Curiously, McLaren et al. (1989) 'observed copious egg production by females (of *M. lucens*) soon after being brought to the laboratory' (p. 569) but never determined their EPR.

Table 1. *Metridia pacifica*. The relationship between specific egg production (SEP) and chlorophyll *a* (Chl) after standardizing rates to 5°C. SEP_{max} is the food-saturated SEP. K_d is the chlorophyll concentration at half saturation. The exponent *b* is simply a fitted parameter. $p < 0.0001$ for all relationships

| Function | Equation | $SEP_{max} \pm SE$ | $K_d \pm SE$ | Exponent | Adjusted r^2 |
|--------------------------------------|---|--------------------|-----------------|-----------------|----------------|
| Michaelis-Menten (all data) | $SEP = \frac{SEP_{max} Chl}{(K_d + Chl)}$ | 0.17 ± 0.03 | 1.46 ± 0.52 | | 0.59 |
| Michaelis-Menten (1 outlier removed) | $SEP = \frac{SEP_{max} Chl}{(K_d + Chl)}$ | 0.18 ± 0.03 | 1.53 ± 0.45 | | 0.69 |
| Chapman | $SEP = SEP_{max} (1 - e^{-K_d Chl})^b$ | 0.17 ± 0.02 | 1.24 ± 0.46 | 2.01 ± 0.76 | 0.82 |
| Hill | $SEP = \frac{SEP_{max} Chl^b}{(K_d^b + Chl^b)}$ | 0.18 ± 0.02 | 1.02 ± 0.18 | 1.95 ± 0.47 | 0.83 |

Table 2. Comparison of egg production towers to other egg production methods, such as individuals in multi-wells, individuals in 250 ml bottles or groups of 4 females in 1000 ml flasks. Preliminary experiments in multi-wells alone presented for comparison. EPR: egg production rate

| | Method | No. of females | No. of clutches | Clutch size | First clutch (% normal) | Second clutch (% normal) | EPR |
|----------------|-------------|----------------|-----------------|----------------|-------------------------|--------------------------|------|
| May-02 (Gak4) | Towers | 48 | 49 | 53.1 ± 3.6 | 59 | 88 | 37.3 |
| | Multi-wells | 48 | 43 | 23.5 ± 4.0 | 94 | 93 | 12.2 |
| May-04 (Gak4) | Towers | 48 | 32 | 36.0 ± 2.0 | 68 | 79 | 24.0 |
| | Multi-wells | 48 | 13 | 11.9 ± 1.6 | 100 | 99 | 3.2 |
| | Bottles: 1φ | 39 | 8 | 12.8 ± 2.5 | — | — | 2.6 |
| | Flask: 4 φ | 40 | — | — | — | — | 2.4 |
| May-04 (Gak10) | Towers | 48 | 27 | 41.8 ± 2.1 | 9 | 1 | 23.5 |
| | Bottles: 1φ | 39 | 12 | 7.5 ± 2.7 | — | — | 2.3 |
| | Flask: 4 φ | 40 | — | — | — | — | 4.8 |
| Apr-01 (PWS2) | Multi-wells | 57 | 25 | 8.4 ± 1.2 | 94 | — | 3.7 |
| May-01 (PWS2) | Multi-wells | 40 | 0 | — | — | — | 0 |
| July-01 (Gak1) | Multi-wells | 40 | 0 | — | — | — | 0 |
| July-01 (PWS2) | Multi-wells | 40 | 0 | — | — | — | 0 |

Compared to other studied species, observations from all *Metridia* species yield rates that would be reconcilable with our observations that *M. pacifica* and *M. okhotensis* egg production is not adequately assessed by traditional methods. If such a generalization is correct, undoubtedly, this has contributed to the impression that *Metridia* has unusually low egg production. Averaged over all experiments, 49% of the *M. pacifica* eggs did not develop normally, and would not have been recovered if they had been concentrated by screening down the experiment rather than observing them where they were laid. In a side-by-side methodological comparison, standard methods underestimated EPR by 3- to 10-fold. In fact, the determination of unacceptably low egg production by some researchers has either discouraged them from publishing their results, and/or stifled their interest in more routine determination of egg production for *Metridia* spp.

Under experimental conditions, eggs without membranes consistently failed to undergo normal development and hatch. It is unclear whether abnormal development is reflective of what is happening in the water column, or only in the experiments. It is unlikely that a methodological artifact is solely responsible for the fragility or lack of egg membranes. In concurrent experiments with other calanoid species and the same techniques, abnormal development was either absent or minimal. If the methodology is responsible for abnormal development in *Metridia* spp. eggs, then one would not expect the problem to disappear during the summer. Furthermore, during the spring, when membranes are typically absent, we observed eggs that lack a membrane even immediately after being laid. Although incubation temperatures are lowest during spring, when bad eggs are most common, *Metridia* spp. does not have problems with spring recruitment and population maintenance in the study area or over its entire sub-arctic range (e.g. Batchelder 1985, Vidal & Smith 1986, Hirakawa & Imamura 1993, Padmavati et al. 2004), so cold temperatures are not likely to be the problem. Conversely, one would expect the developmental problem to be magnified at higher temperatures, when developmental rates are maximal; yet, this is when development proceeds most successfully.

This leaves the possibility that either a key nutritional requirement is absent in the diet (or the animal's lipid stores), or that some element in the diet interferes with the production of normal eggs during the spring. There has been active debate for over a decade that when diatoms dominate the phytoplankton community, egg production and viability are negatively impacted due to adverse chemicals (e.g. Miralto et al. 1999, 2003, Irigoien et al. 2002). Although we cannot preclude that chemicals in prey such as diatoms are responsible (Ianora et al. 2004), such chemicals appear

to have a limited or less obvious impact on other species that are reproductively active concurrently in the Gulf of Alaska during the spring 'bloom'. *Metridia* species may simply be more susceptible than other co-occurring species to the aldehydes produced by diatoms. Alternatively, the problem could be due to the absence of some element in the diet; one that is not stored along with the large lipid stores commonly observed in March, April and, to a lesser extent, May. In the latter scenario, females that have the energetic reserves after over-wintering begin to produce eggs, but essential compounds required for the production of a normal egg membrane (and potentially other cellular functions) are missing. Future activities will be directed towards examining the relationship between the prevalence of diatoms and abnormal eggs.

Regardless of the underlying cause, it is clear that the standard techniques developed for estimating egg production, may not be appropriate for all species of copepods. We now have a rough framework of the relationship between (female) growth rate (Hirst & Bunker 2003) or fecundity (Bunker & Hirst 2004), temperature, body size, and resources that allow us to see whether experimental data are consistent with these patterns. The data in this study are clearly consistent with the forms of those relationships. When data appear anomalous, or even paradoxical, as may be the case with all *Metridia* species, methodology should be more closely scrutinized before such rates are simply considered 'exceptions to the rule'.

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LITERATURE CITED

- Batchelder HP (1985) Seasonal abundance, vertical distribution, and life history of *Metridia pacifica* (Copepoda: Calanoida) in the oceanic subarctic Pacific. *Deep-Sea Res* 32:949–964
- Batchelder HP, Miller CA (1989) Life history and population dynamics of *Metridia pacifica*: results from simulation modelling. *Ecol Model* 48:113–136
- Brodsky KA (1967) Calanoida of the far-eastern seas and the polar basin of the USSR. Israel Program for Scientific Translations, Jerusalem
- Brodsky KA (1977) The description of male *Metridia okhotensis* Brodsky (Calanoida, Metridiidae). In: Brodsky KA, Vyshkartseva NV (eds) Marine plankton (systematics and faunistics). Explorations of the marine fauna, 20. Leningrad, p 4–5 (in Russian)
- Bunker AJ, Hirst AG (2004) Fecundity of marine planktonic

- copepods: global rates and patterns in relation to chlorophyll a temperature and body weight. *Mar Ecol Prog Ser* 279:161–181
- Buskey EJ, Stearns DE (1991) The effects of starvation on bioluminescence potential and egg release of the copepod *Metridia longa*. *J Plankton Res* 13:885–893
- Cooney R, Coyle KO, Stockmar E, Stark C (2001) Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. *Fish Oceanogr* 10(Suppl 1):97–109
- Coyle KO, Pinchuk AI (2003) Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. *Fish Oceanogr* 12:327–351
- Coyle KO, Paul AJ, Ziemann DA (1990) Copepod populations during the spring bloom in an Alaskan subarctic embayment. *J Plankton Res* 12:759–797
- Downing JA, Rigler FH (1984) A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific, London
- Gardner GA, Szabo I (1982) British Columbia pelagic marine Copepoda: an identification manual and annotated bibliography. *Can Spec Publ Fish Aquat Sci* 62:1–536
- Hansen B, Christiansen S, Pedersen G (1996) Plankton dynamics in the marginal ice zone of the central Barents Sea during spring: carbon flow and structure of the grazer food chain. *Polar Biol* 16:115–128
- Hay SJ, Kjørboe T, Matthews A (1991) Zooplankton biomass and production in the North Sea during the Autumn Circulation Experiment, October 1987–March 1988. *Cont Shelf Res* 11:1453–1476
- Hirakawa K, Imamura A (1993) Seasonal abundance and life history of *Metridia pacifica* (Copepoda: Calanoida) in Toyama Bay, southern Japan Sea. *Bull Plankton Soc Jpn* 40:41–54
- Hirst AG, Lampitt RS (1998) Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Mar Biol* 132:247–257
- Hirst AG, Bunker AJ (2003) Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature, and body weight. *Limnol Oceanogr* 48:1988–2010
- Hopcroft RR, Clarke C, Chavez FP (2002) Copepod communities in Monterey Bay during the 1997 to 1999 El Niño and La Niña. *Prog Oceanogr* 54:251–263
- Huntley ME, Escritor F (1992) Ecology of *Metridia gerlachei* Giesbrecht in the western Bransfield Strait, Antarctica. *Deep-Sea Res* 39:1027–1055
- Ianora A, Miralto A, Poulet SA, Carotenuto Y and 8 others (2004) Aldehyde suppression of copepod recruitment in blooms of a ubiquitous planktonic diatom. *Nature* 429:403–407
- Incze LS, Siefert DW, Napp JM (1997) Mesozooplankton of Shelikof Strait, Alaska: abundance and community composition. *Cont Shelf Res* 17:287–305
- Irigoin X, Harris RP, Verheye HM, Joly PB and 14 others (2002) Copepod hatching success in marine ecosystems with high diatom concentrations. *Nature* 419:387–389
- Kjørboe T, Sabatini M (1994) Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods. *J Plankton Res* 16:1353–1366
- Mauchline J (1998) The biology of calanoid copepods. *Advances in marine biology*, Vol 33. Academic Press, London
- McLaren IA, Tremblay MJ, Corkett CJ, Roff JC (1989) Copepod production on the Scotian Shelf based on life-history analyses and laboratory rearings. *Can J Fish Aquat Sci* 46:560–583
- Miralto A, Barone G, Romano G, Poulet SA and 6 others (1999) The insidious effect of diatoms on copepod reproduction. *Nature* 402:173–175
- Miralto A, Guglielmo L, Zagami G, Buttino I, Granata A, Ianora A (2003) Inhibition of population growth in the copepods *Acartia clausi* and *Calanus helgolandicus* during diatom blooms. *Mar Ecol Prog Ser* 254:253–268
- Nielsen TG, Richardson K (1989) Food chain structure of the North Sea plankton communities: seasonal variations of the role of the microbial loop. *Mar Ecol Prog Ser* 56:75–87
- Ozaki K, Takeuchi T, Shiga N, Mito K (2001) Winter zooplankton biomass and population structure of calanoid copepods in the Bering Sea basin. *Plankton Biol Ecol* 48:46–51
- Padmavati G, Ikeda T (2002) Development of *Metridia pacifica* (Crustacea: Copepoda) reared at different temperatures in the laboratory. *Plankton Biol Ecol* 49:93–96
- Padmavati G, Ikeda T, Yamaguchi A (2004) Life cycle, population structure and vertical distribution of *Metridia* spp. (Copepoda: Calanoida) in the Oyashio region (NW Pacific Ocean). *Mar Ecol Prog Ser* 270:181–198
- Rebstock GA (2001) Long-term stability of species composition in calanoid copepods off southern California. *Mar Ecol Prog Ser* 215:213–224
- Richardson AJ, Verheye HM, Herbert V, Rogers C, Arendse LM (2001) Egg production, somatic growth and productivity of copepods in the Benguela Current system and Angola-Benguela Front. *S Afr J Sci* 97:251–256
- Roff JC, Hopcroft RR (1986) High precision microcomputer based measuring system for ecological research. *Can J Fish Aquat Sci* 43:2044–2048
- Runge JA, Roff JC (2000) The measurement of growth and reproductive rates. In: Harris RP, Weibe PH, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, London, p 401–454
- Schnack-Schiel SB (2001) Aspects of the study of the life cycles of Antarctic copepods. *Hydrobiologia* 453/454:9–24
- Shebanova MA (1977) Distribution and age composition of *Metridia okhotensis* and *Metridia pacifica* (Copepoda: Calanoida) in epipelagic of the Okhotsk Sea. *Izvestia TINRO* 122:361–373 (in Russian)
- Sherman K, Solow A, Jossi J, Kane J (1998) Biodiversity and abundance of zooplankton of the Northeast Shelf ecosystem. *ICES J Mar Sci* 55:730–738
- Smith SL, Vidal J (1986) Variations in the distribution, abundance, and development of copepods in southeastern Bering Sea in 1980 and 1981. *Cont Shelf Res* 5:215–239
- Vidal J, Smith SL (1986) Biomass, growth and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. *Deep-Sea Res* 33:523–556
- Weingartner TJ, Coyle KO, Finney B, Hopcroft RR and 15 others (2002) The Northeast Pacific GLOBEC program: coastal Gulf of Alaska. *Oceanography* 15:48–63