Copepod growth in detail: pattern similarity to decapod larvae

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It is proposed that copepods grow between one moult and the next in much the same fashion as established by Klaus Anger and others for decapod crustacean larvae. The analogy is justified by commonality of (i) approximately isochronal development patterns, (ii) potential for continuously exponential growth at stage-to-stage resolution, and (iii) demonstrated points of reserve saturation. Thus, as for crab zoeae, the copepod pattern should be very fast initial growth, then slowing as activity shifts to preparation of the new exoskeleton prior to moult. As much as 80% of growth may occur in the first half of the moult cycle, with no growth at all in the last third. Establishing the exact patterns for copepods faces difficulties not presented by decapod larvae, and some solutions to these problems are suggested. Obtaining precise data will help to predict and interpret (model correctly) the effects of food limitation in the field.

Keywords: biomass determination, copepod, growth pattern, point of no return, point of reserve saturation.

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Likely copepod growth patterns

> In order to appreciate the role of zooplankton in material flow and transformation in the sea, it is essential that their rates of growth and production can be determined and the factors of control understood.
>
> Hirst and Lampitt (1998)

Planktologists have taken particular interest in copepod growth patterns, stimulated in part by the search for a shortcut to secondary production estimation for this crustacean group (Huntley and Lopez, 1992; Hirst and Sheader, 1997; Hirst and Lampitt, 1998; Hirst and Bunker, 2003; Hirst *et al.*, 2003, 2005). That is because copepods are consistently a dominant proportion of the mesozooplankton in oceans and lakes, and mesozooplankton are important in the foodwebs leading to harvestable, large animals (primarily fish and squid). Despite this interest, available approximations of growth rates for copepods in the field remain crude and unreliable. I propose that good dividends could derive from learning the growth patterns of copepods with more precision than has been applied to date, particularly for the copepodite stages responsible for a major share of mesozooplankton tissue production. Initially at least, the work must be done on laboratory stocks, with transfer of implications to field results. The basic notion, proposed earlier by Carlotti and Nival (1991, 1992), and Crain and Miller (2001), is that copepods add biomass at rates strongly varying through their moult cycles in patterns similar to those demonstrated for crab larvae by Klaus Anger and others (Anger and Dawirs, 1981; Anger and Spindler, 1987; Anger and Ismael, 1997; reviews in Anger, 1998, 2001).

Crab larvae offer strong advantages for determining within-stage growth patterns compared with copepods. Many female crabs carry their eggs attached to their abdomen or abdominal legs until they hatch as zoeae, at a stage of development comparable to the copepodite stages of copepods. These larvae begin to feed, gain weight, and moult. Hatching in many or most species occurs in near synchrony that is sustained through several moults. Thus, a clutch can be progressively sacrificed to determine the time course of biomass increase. Individual variability can be modest because the eggs in a clutch are full siblings, so biomass determinations can be made for counted groups. A graph (Figure 1) from Anger (1998, 2001) gives the pattern for Zoea I of the spider crab *Hyas araneus*. Growth is very rapid at first, with 82% of the total stage dry-weight increment laid up in the first half of the moult cycle. Then growth slows, presumably because morphogenetic preparation for the next moult takes up more of the ingested nutrition. In the final 30% of the moult-to-moult interval, there is no growth at all in the sense of biomass increase. Ingestion and assimilation also decrease markedly after about half of the interval.

Specific points in this larval-crab growth pattern are associated with aspects of the moult cycle (reviewed in Anger, 2001). Completion of an initial fraction of moult-cycle growth, usually an increase of 60–70% over biomass at moult that is accomplished in only 20–30% of the moult cycle, is associated with initiation of the premoult sequence of epidermal events. This transition is often designated D0 in a scheme of epidermal stages A to E: A, initial post-moult during body expansion by drinking; B, exoskeletal thickening by secretion of additional chitin; C, intermoult; D, premoult divided into substages of formation of new exoskeleton; E, ecdysis. The first localized separation of epidermis from the exoskeleton (apolysis), usually around the tips of limbs bearing long setae, occurs in D0. There is tight, hormonally controlled correlation among these stages to the division phases (M, G1, S, G2) of cells multiplying for epidermal expansion and presumably for increasing segmentation and other complexity (Freeman, 1993).

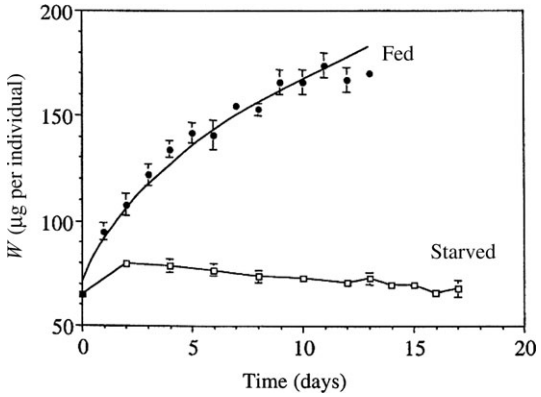

Figure 1. The growth pattern of the first zoeal stage of *Hyas araneus*, the European spider crab, with individual biomass measured as dry weight, *W*. The figure is from Anger (1998, 2001; reproduced with permission from Balaban, Rehovot, Israel, and K. Anger). Note that ~80% of growth occurs in the initial half of the moult cycle, and essentially no growth occurs in the final 30%. The open squares represent data showing no growth in the absence of food.

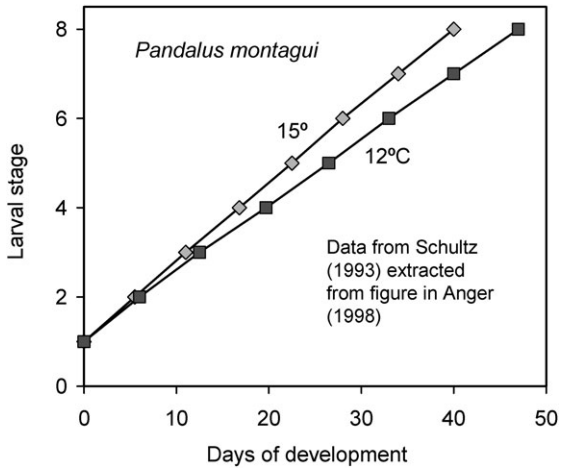

Figure 2. The isochronal development pattern of *Pandalus montagui* at 12°C and 15°C. Data are from Schultze (1993); values were extracted from Anger (1998). More temperatures are represented in the original data, all sustaining isochronal development.

Significantly for the comparison with copepods, D0 in crabs is associated with a "point of reserve saturation" (PRS), after which moulting will proceed to the next instar even if food is entirely withdrawn at any subsequent time. Transition from C to D0 is hormonally controlled, an event likely enabled by passing a rather definite tissue-mass to body-volume ratio, a triggering condition factor. The existence of PRS is an important feature of decapod larval development (Anger and Dawirs, 1981; Anger *et al.*, 1981; Dawirs, 1984, 1986; Anger and Spindler, 1987; Staton and Sulkin, 1991; Abrunhosa and Kittaka, 1997; Anger, 2001). The exact timing varies among species, but for many, withdrawal of all food at only ~30% of the moult-to-moult interval will not inhibit moulting to the next stage. By PRS, the larva has been hormonally triggered to complete exoskeleton development and to moult. If the larva is fed immediately after such a moult during starvation, some extra time will be required for it to recover and complete the next stage, and mortality rates are typically somewhat enhanced (Anger and Dawirs, 1981).

Decapod crustacean larvae also have a point of no return (PNR; Anger and Dawirs, 1981; Anger *et al.*, 1981; Dawirs, 1984, 1986; Staton and Sulkin, 1991; review in Anger, 2001; Paschke *et al.*, 2004). If not fed for a sufficiently long interval after a moult, they will not be able to resume growth even when given copious food, and they die. The character of a possible PNR in copepod development remains to be established, as discussed at the end of this paper.

An analogy between within-stage growth patterns in copepods and those of decapod larvae is supported by three strong similarities already established. First, both have roughly constant stage durations, so called isochronal development (Miller *et al.*, 1977). There has been much debate about this in regard to copepods (e.g. Landry, 1983), and there are deviations. For example, when N3 is the first-feeding naupliar stage, which is typical of broadcast spawning forms like *Calanus*, it is longer than the other naupliar stages, particularly longer than N1 and N2. There is usually also definite extension of intermoult intervals at the last copepodite stages in *Calanus* and many other species, particularly extension of C5. However, data for *Calanus agulhensis* and *Calanoides carinatus* (Peterson and Painting, 1990) and for *Calanus finmarchicus* (Campbell *et al.*, 2001) demonstrate that the main sequence of development, even in Calanidae, has nearly constant intervals. A good demonstration of the isochronality of decapod larvae is shown by Anger (1998, Figure 2 here), based on data from a thesis by Schultze (1993) for *Pandalus montagui*. That shrimp moults at remarkably equal intervals as it passes through eight larval stages.

Second, looked at on a stage-to-stage basis (as opposed to durations within the moult cycle), both decapod larvae and copepods add biomass approximately exponentially, when provided with replete nutrition. A good example for decapods is the larval growth pattern of the saltmarsh crab *Chasmagnathus granulata*, which, at Zoea I, II, III, IV, Megalopa, and Crab I, has dry weights of, respectively, 190, 356, 757, 1661, 3211, and 5468 µg, increasing about twofold per stage (Anger and Ismael, 1997). Many pelagic, calanoid copepods can add biomass at nearly constant, exponential rates through all or most of their development, if they are fed a replete and qualitatively suitable diet. Again, there are deviations: (i) non-feeding, early naupliar stages lose weight rather than grow; (ii) possibly growth is slower during the metamorphosis between the sixth naupliar and first copepodite stages (e.g. *Acartia*, Miller *et al.*, 1977); and (iii) it is likely that storage lipid added in late stages increases body mass at a rate different from early body growth. However, the literature provides many examples of (or approximately of) exponential growth. As a small sample, *Acartia hudsonica* (Landry, 1978), *Acartia californiensis* (Miller *et al.*, 1977), *Pseudodiaptomus marinus* (Uye *et al.*, 1983), and *Pseudocalanus newmani* (Lee *et al.*, 2003) add weight in roughly constant ratios between stages. The excellent data of Vidal (1980a, b) and Campbell *et al.* (2001) for two different species of *Calanus* show closely exponential initial growth, then slowing in the last stages, C4 and C5.

There are some datasets that seem to show copepod growth that is even more extreme than continuously exponential. Consider the growth pattern of *Pseudodiaptomus hessi* found by Jerling and

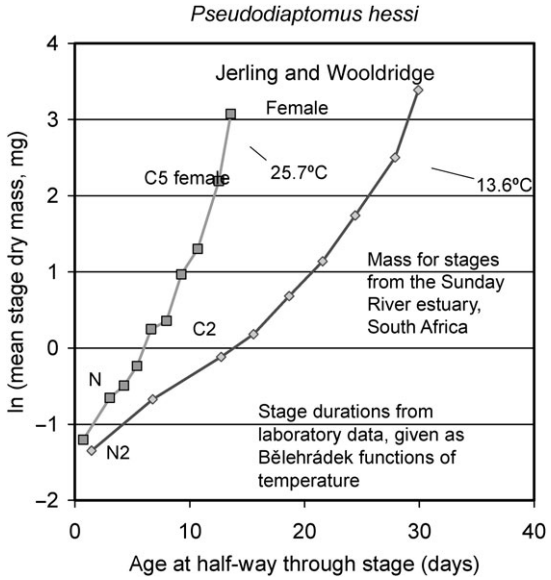

Figure 3. Individual biomass vs. development time of *Pseudodiaptomus hessi,* based on data in Jerling and Wooldridge (1991). Weights are means for the stage; time is the sum of tabled Bělehrádek functions developed by Jerling and Wooldridge for each of the stages. Growth with replete nutrition appears to be in progressively larger ratios with advancing stages.

Wooldridge (1991; Figure 3). Their dataset has the advantage that the animals were actually weighed, rather than including weights based on a general weight-to-length ratio (Rey-Rassat *et al.*, 2004, stress the importance of this). However, weights were determined after quite long preservation, and age was determined by me for the figure by summing stage durations provided by Jerling and Wooldridge (1991) as Bělehrádek functions determined in the laboratory. Therefore, some uncertainty remains about actual weight-at-age. The food regime, however, was just the particulate contents in water from the Sundays River estuary, South Africa, where the *P. hessi* were collected.

Third, both decapod larvae and copepodites have a PRS early in each moult cycle. For crabs and lobsters, PRS has been explicitly demonstrated (citations above). The demonstration in copepods is less refined. Copepodites of a given stage collected at sea and placed in filtered seawater (starved) will continue to moult until remarkably large percentages have reached the next stage. In experiments with *Calanus pacificus* C4 collected close to the California coast (Miller *et al.*, 1984, their Figures 3, 4, 6, 8, 9), the fractions moulting rose progressively over 2 days to typically 50–70% of the numbers initially sorted. Clearly, copepodites have exactly the same capacity as crab zoeae to establish a PRS very early in the moult cycle.

Based on these similarities, decapod larvae are a good model for the detailed growth pattern of copepodites.

Obtaining copepod growth patterns at within-stage detail

We lack the datasets necessary to examine copepodite biomass increase at within-stage resolution. Almost inevitably, such data must be developed by laboratory rearing. For just one copepodite stage (e.g. C3), the data would be a table, for a statistically adequate number of individuals distributed throughout the age range of the stage, of (i) exact age-within-stage (time since the prior moult), (ii) biomass as dry weight or carbon content, and (iii) body volume or at least body length. We lack such data because, on the whole, it has not been possible to raise groups in sufficient moulting synchrony for a stage to have narrow variance in age added since the last moult (e.g. Sciandra, 1986; Peterson and Painting, 1990; discussed by Lopez, 1991). However, Campbell *et al.* (2001) nearly obtained developmental synchrony with cohorts of *Calanus finmarchicus* reared on a diet apparently close to ideal. They did not determine within-stage biomass increments, but another rearing with equal synchrony might allow it.

In addition, individuals are too small in many species and stages for biomass determination on single specimens. Readily available measurement techniques (dry weights by electro-balance, carbon analysis, etc.) are not sensitive enough for specimens of any but the largest stages of large species. The biomass measures need to be precise to within a few per cent. Length is needed because overall body size varies in a given stage by substantial ratios; for example, length of *Calanus finmarchicus* C5 varies by a factor of 1.7 and body volume by a factor of ~4 (Miller *et al.*, 2000).

Despite these difficulties, there are ways forward to define the copepod growth pattern with higher resolution than is currently available (4-h resolution by Carlotti and Nival, 1991). A system has been developed at Oregon State University to take digital pictures every six minutes of each of 24 female copepods in dishes (Miller *et al.*, *in litt.*). The pictures have allowed us to determine to within 6 min (0.1 h) when clutches of eggs are produced. The 24 dishes, mounted on plexiglas sleeves hanging from a motor-driven carousel, are pulled around an annular plexiglas trough filled with precisely temperature-regulated water once every 6 min. As each dish passes the camera that is focused on its bottom, the camera takes a picture and transfers it to a computer server. Modern digital storage capacity allows thousands of pictures to be accumulated at reasonable cost, and they can be scanned at suitable intervals to determine the timing of the events they record. In place of spawning dishes, beakers containing one copepodite with a replete diet can be hung from the carousel. New moults sink and are visible in the photographs of the beaker bottoms. Time marks on the photos (or times recorded with the computer files) will show when new moults first appear and thus determine the time at zero age within the new stage. Once the moulting times of a set of copepodites are known, suitable ages after the moult can be assigned for determining biomass. More than one camera arrangement can be imagined, perhaps a system with the camera moving rather than the dishes that could take recurring pictures of many more than 24 specimens.

Then, because of the effect of body size (body volume = f[body length]) on biomass, weights must be determined for each single specimen. Biomass could be dry weight determined with a balance, or it could be carbon content. Dry weight determinations of single individuals will only be feasible for larger copepods. For example, the C3 of *Acartia* will grow from ~0.8 to ~1.8 μg, considerably less than the weights of the tared metallic foils needed for drying and weighing them. Very good practice with an electrobalance will provide weights to ±0.2 μg, at best, considering the error propagation of the tare weighing and tare–animal weighing. For purposes of determining small increments of growth through the moult cycle, these errors of 10–25% are far too large. Suitably precise results can probably be obtained for the copepodite stages of larger species. The C3 of *Calanus* will grow from ~25 to ~45 μg, for which the precision of weighing is sufficient to provide a very good within-stage growth sequence.

An appealing alternative is direct carbon analysis. Salonen (1979) reported the development of a high-temperature carbon analyser that, he claimed, could be calibrated to estimate minuscule amounts of carbon, down to 0.01 μg without sample weighing. The analytical device was a catalytic furnace, comparable with that in any CHN analyser, burning samples with high-purity oxygen. Water was condensed from the resulting mixture of gases, and carbon was determined by non-dispersive infrared (NDIR) detection of the CO_2 content. Consequently, NDIR analysis of carbon at the necessary sensitivity is certainly possible, and the current generation of Schimadzu machines (e.g. their TOC-VCS/TOC-VCP model) applying oxidation and NDIR can determine as little as 4 ng of carbon in small water (or seawater) samples (~100 μl). However, Schimadzu's furnace attachment for solid samples requires 100 μg of carbon, which is too much, about equivalent to the content of an adult *Calanus*. The combustion gases from the furnace of a standard CHN analyser could be redirected to a suitable NDIR detector, and suitable detectors are available. A machine of the necessary combined capability is not currently on the market, although one could be built to determine the growth pattern of copepods.

If the basic weight-at-age for a suitable stage can be obtained, combining the suggestions above, then a way must be found to account for the effect on biomass of variation in body volume or linear dimensions. After that standardization, a sort of standardized "Anger graph" (like Figure 1) could be developed for copepods. For example, something like the approximate formula for body volume as a function of length in *C. finmarchicus* C5, which was developed by Miller *et al.* (2000) from optically determined dimensional data, could be applied. That is,

$$\text{Body Volume} = 0.0292\ (\text{Prosome Length})^{3.67}.$$

The exponent larger than 3.0 implies that shape is not constant with size, that longer bodies are relatively wider. Weights at specific ages-within-stage could be compared as ratios with volumes estimated by such a function from simple length measures. Species- and stage-specific volume = *f*(length) models would be needed and probably can be developed directly from the age–length–mass tables for the copepodite stage under study. The resulting data can be expected to follow a curve like that in Figure 4, which is just a representation of the analogy to decapod larvae.

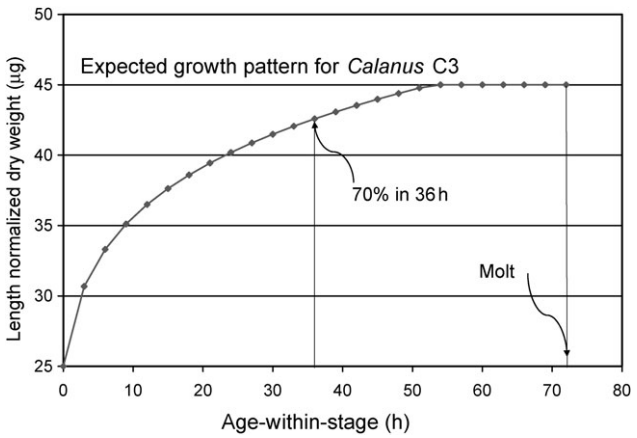

Figure 4. Expected (theoretical) growth pattern for C3 of *Calanus* (e.g. *C. marshallae*) after normalizing to the body volume of animals at 2.3 mm prosome length.

The observations can readily be extended to determine the PRS for copepodites. After different intervals with replete nutrition, the animals would be transferred to filtered seawater and their subsequent moulting (or failure to moult) monitored. PRS would likely be reached at ~30% of the moult-to-moult interval, or when the animal had reached approximately three-quarters of its fully fed final weight. It should also be possible to examine the interaction of varying nutrition levels with the growth pattern and to define PRS in terms of weight or condition factor, rather than in terms of the required duration of initial feeding on a replete diet to establish reserve saturation. The latter has consistently been the form of data for identifying PRS in decapod larvae. A growth-limiting diet might well allow an animal to reach PRS, but only after an extended period.

Discussion

If someone is persuaded by this argument to obtain the data for determining the growth dynamics of pelagic copepods at high within-stage resolution, what will we gain? Clearly, it can be done, but the necessary miniaturization of the measurements means that it will be difficult. What would the field gain by having this information? Why is the analogy to decapod larvae not sufficient to inform our studies on the role of copepods in pelagic ecology?

Copepods are the archetypal mesozooplankton, so they represent that whole trophic complex in many ecosystem models (e.g. Landry, 1975; Steele, 1998; Steele and Clarke, 1998; Peña, 2003; Lancelot *et al.*, 2005). Moreover, copepod developmental timing is important in many models of their population dynamics (e.g. van den Bosch and Gabriel, 1994; Miller *et al.*, 1998; Carlotti and Wolf, 1998; Speirs *et al.*, 2006). However, both classes of model generally apply imprecise growth mechanics (or none). The partial uncoupling of biomass growth from stage-to-stage development implied by the PRS phenomenon means that fully representative models, especially those invoking food limitation, should include detailed representation of the timing and nutritional responses of growth.

Food limitation commonly affects mesozooplankton, and among copepods it almost certainly affects older stages preferentially (Hirst *et al.*, 2003). Because of the PRS phenomenon, it can be seen in the field in the proportions of individuals in different tooth-formation stages (Crain and Miller, 2001). After the onset of near-starvation, individuals accumulate in the post-moult phases of successive stages, whereas later moult-cycle stages disappear. Initiation of tooth development in copepodites apparently occurs at the same stage in development as PRS, much as PRS is closely coupled to the D0 stage (initial integument apolysis) of the decapod moult cycle (Anger and Spindler, 1987). Much effort has gone into understanding food limitation effects on copepods, particularly work by Vidal (1980a, b) and Klein Breteler *et al.* (2004 and references therein), but that work lacked a refined, underlying model of growth and development mechanics. We could draw a suitable model from the analogy to decapods, but it would be better to have real, copepod-specific data.

As stated in the initial paragraphs, if a decapod larva is subjected to a period of starvation soon after moult and if that persists long enough, the larva will not recover its capacity to eat and grow when food reappears. It dies. It has passed the PNR. Certainly, copepods also exhibit such limits on their ability to recover from starvation, limits with the potential to remove important trophic components from pelagic ecosystems. Sometimes such

removal will be in process while the animals are still alive to be captured in plankton samples, misleading observers about the effective and future trophic relations in the ecosystem. Techniques for experimentation with copepodites of accurately known age-within-stage will allow more precise study of starvation and malnutrition effects on copepod growth, including probabilities for recovery and the extent of developmental delays. We know from work on starvation in adults and C5 (e.g. Dagg, 1977; Koski and Klein Breteler, 2003) that different species differ strongly in their ability to persist through and recover from starvation; those with substantial storage lipids survive longer. There are also studies of adult females in which recovery of egg production after starvation events was the issue of concern (e.g. Niehoff, 2000).

It is likely that starvation has different effects on naupliar and copepodite stages. Tsuda (1994), for example, showed that copepodites of *Pseudocalanus newmani* survive longer without food than nauplii, but, short of dying, their capacity to recover once food is again available (i.e. the existence of a PNR) remains unknown. Lopez (1996) has performed an approximate determination of PNR in naupliar stages of *Calanus pacificus* that were fed, or not fed, with a culture of *Procentrum minimum*. She states "... survivorship and development rate during the remaining naupliar stages were reduced when initial feeding was delayed for ~10 h after moulting to N3. In otherwise well fed stages N3–N6, development and survival were reduced after starvation periods >6 h and >14 h, respectively...".

There are effects of starvation on copepods comparable with the decapod PNR, and Lopez cites Anger *et al.* (1981) in making that association. Starvation effects similar to PNR have been modelled for copepods by Batchelder *et al.* (2002), replacing the notion of a tolerable duration of starvation with a minimum survival weight approached by modelled catabolism. Probably a minimum weight (or condition factor) is a better form of data than has usually been provided for decapod larvae (or for *Calanus* nauplii by Lopez), where PNR has only been characterized as the fatal duration of complete absence of food before a standard replete diet is provided. It is likely that minimum survival weights or condition factors could be discovered by experiments with animals of known age-within-stage. Determinations of PNR by Paschke *et al.* (2004) for early larvae of *Crangon* show that starvation resistance varies seasonally, with larvae from larger winter eggs better able to recover from longer starvation than those from smaller summer eggs. Thus, time to PNR is certainly more complex than has been demonstrated for either meroplankton or holoplankton, varying with every aspect of nutrition: food quantity, quality, timing of availability (e.g. Gimenez and Anger, 2005), and parental investment in eggs. PNR is certain to exist in copepods, for copepodite stages as well as nauplii. Both its timing and the low food levels inducing it should be determined. Doing that in light of high-resolution growth patterns will show us the details of the interaction of copepods with the nutrition available in their habitat.

From the decapod analogy, we know that copepodite growth rate almost certainly varies through the moult cycle, even with replete nutrition. Less certainly but very likely, rates of feeding and metabolism will also vary with moult phase. Therefore, correct interpretation of copepod physiological data requires attention to the moult-cycle phase of observed copepodites. In many cases, copepods develop in temporally focused cohorts; for high-latitude populations, these are annual or biennial cohorts. If we collect, say, C4 of a species of interest for measurements of rates, the age-within-stage composition will very likely advance with the progress of the seasons, i.e. with the developmental advance of the population cohort. Therefore, measured rates will also vary. Possibly, the age-within-stage composition of a population at the moment it is studied could be approximated from proportions of tooth-development stages (Crain and Miller, 2001). For example, the decapod analogy (Figure 1) suggests that a stock of copepodites all at older ages within their stage (all with new teeth forming on the epidermis of the gnathobases) is likely to have lower feeding rates than stocks at younger ages. Because late-phase animals would not be adding weight, they would be feeding very slowly.

In sum, knowing the detailed growth dynamics of copepods will lead to better understanding of pelagic ecology. The analogy with decapod crustaceans suggests that growth in each instar will be rapid initially, then slow and later stop well before the moult from the stage. Exoskeletal morphogenesis takes place during the final phase. The requirements for such studies of copepods are more difficult than for studies of crab or shrimp larvae, but collecting suitable data is possible. Application of the decapod larval analogy does not, unfortunately, suggest that demonstrating the within-stage growth patterns of copepods will return us to a simple, reliable method for estimating the secondary production attributable to a given species or stage of planktonic copepods. That Holy Grail of mesozooplankton ecology will likely remain hidden awhile. However, understanding within-stage growth processes will help us to explain why copepod development is less food-sensitive than growth and to predict the effects of that on size distributions. It will provide tools to demonstrate starvation when it occurs in the field and for assessing the effects of nutrition on mortality patterns. It will help to explain the outcomes of moulting-rate determinations and other field-based evaluations that are affected by cohort structure. The insights will branch out in many directions.

References

Abrunhosa, F. A., and Kittaka, J. 1997. Effect of starvation on the first larvae of *Homarus americanus* (Decapoda, Nephropidae) and phyllosomas of *Jasus verreauxi* and *J. edwardsii* (Decapoda, Palinuridae). Bulletin of Marine Science, 61: 73–80.

Anger, K. 1998. Patterns of growth and chemical composition in decapod crustacean larvae. Invertebrate Reproduction and Development, 33: 159–176.

Anger, K. 2001. The Biology of Decapod Crustacean Larvae. Balkema Publishers, Lisse. 402 pp.

Anger, K., and Dawirs, R. R. 1981. Influence of starvation on the larval development *Hyas araneus* (Decapoda, Majidae). Helgoländer Wissenschaftliche Meeresuntersuchungen, 34: 287–311.

Anger, K., Dawirs, R. R., Anger, V., and Costlow, J. D. 1981. Effects of early starvation periods on zoeal development of brachyuran crabs. Biological Bulletin, 161: 199–212.

Anger, K., and Ismael, D. 1997. Growth and elemental composition (C, N, H) in larvae and early juveniles of a South American salt marsh crab, *Chasmagnathus granulate* (Decapoda: Grapsidae). Mangroves and Salt Marshes, 1: 219–227.

Anger, K., and Spindler, K. D. 1987. Energetics, moult cycle and ecdysteroid titers in spider crab (*Hyas araneus*) larvae starved after the D sub(0) threshold. Marine Biology, 94: 367–375.

Batchelder, H. P., Edwards, C. A., and Powell, T. M. 2002. Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic

success and nearshore retention. Progress in Oceanography, 53: 307–333.

Campbell, R. G., Wagner, M. M., Teegarden, G. J., Boudreau, C. A., and Durbin, E. G. 2001. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Marine Ecology Progress Series, 221: 161–183.

Carlotti, F., and Nival, S. 1991. Individual variability of development in laboratory-reared *Temora stylifera* copepodites: consequences for the population dynamics and interpretation in the scope of growth and development rules. Journal of Plankton Research, 13: 801–813.

Carlotti, F., and Nival, P. 1992. Model of copepod growth and development: moulting and mortality in relation to physiological processes during an individual moult cycle. Marine Ecology Progress Series, 84: 219–233.

Carlotti, F., and Wolf, K-U. 1998. A Lagrangian ensemble model of *Calanus finmarchicus* coupled with a 1-D ecosystem model. Fisheries Oceanography, 7: 191–204.

Crain, J. A., and Miller, C. B. 2001. Effects of starvation on intermolt development in *Calanus finmarchicus* copepodites: a comparison between theoretical models and field studies. Deep-Sea Research II, 48: 551–566.

Dagg, M. 1977. Some effects of patchy food environments on copepods. Limnology and Oceanography, 22: 99–107.

Dawirs, R. R. 1984. Influence of starvation on larval development of *Carcinus maenas* L. (Decapoda: Portunidae). Journal of Experimental Marine Biology and Ecology, 80: 47–66.

Dawirs, R. R. 1986. Influence of limited food supply on growth and elemental composition (C, N, H) of *Carcinus maenas* (Decapoda) larvae, reared in the laboratory. Marine Ecology Progress Series, 31: 301–308.

Freeman, J. A. 1993. The crustacean epidermis during larval development. *In* The Crustacean Integument: Morphology and Biochemistry, pp. 193–219. Ed. by M. N. Horst, and J. A. Freeman. CRC Press, Boca Raton. 231 pp.

Gimenez, L., and Anger, K. 2005. Effects of temporary food limitation on survival and development of brachyuran crab larvae. Journal of Plankton Research, 27: 485–494.

Hirst, A. G., and Bunker, A. J. 2003. Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature, and body weight. Limnology and Oceanography, 48: 1988–2010.

Hirst, A. G., and Lampitt, R. S. 1998. Towards a global model of *in situ* weight-specific growth in marine planktonic copepods. Marine Biology, 132: 247–257.

Hirst, A. G., Peterson, W. T., and Rothery, P. 2005. Errors in juvenile copepod growth rate estimates are widespread: problems with the moult rate method. Marine Ecology Progress Series, 296: 263–279.

Hirst, A. G., Roff, J. C., and Lampitt, R. S. 2003. A synthesis of growth rates in marine epipelagic invertebrate zooplankton. Advances in Marine Biology, 44: 1–142.

Hirst, A. G., and Sheader, M. 1997. Are *in situ* weight-specific growth rates body size independent in marine planktonic copepods? A re-analysis of the global syntheses and a new empirical model. Marine Ecology Progress Series, 154: 155–165.

Huntley, M. E., and Lopez, M. D. G. 1992. Temperature-dependent production of marine copepods: a global synthesis. The American Naturalist, 140: 201–242.

Jerling, H. L., and Wooldridge, T. H. 1991. Population dynamics and estimates of production for the calanoid copepod *Pseudodiaptomus hessei* in a warm temperate estuary. Estuarine and Coastal Shelf Science, 33: 121–135.

Klein Breteler, W. C. M., Koski, M., and Rampen, S. 2004. Role of essential lipids in copepod nutrition: no evidence for trophic upgrading of food quality by a marine ciliate. Marine Ecology Progress Series, 274: 199–208.

Koski, M., and Breteler Klein, W. C. 2003. Influence of diet on copepod survival in the laboratory. Marine Ecology Progress Series, 264: 73–82.

Lancelot, C., Spitz, Y., Gypens, N., Ruddick, K., Becquevort, S., Rousseau, V., Lacroix, G. *et al.* 2005. Modelling diatom and *Phaeocystis* blooms and nutrient cycles in the Southern Bight of the North Sea: the MIRO model. Marine Ecology Progress Series, 289: 63–78.

Landry, M. R. 1975. The structure of marine ecosystems: an alternative. Marine Biology, 36: 1–7.

Landry, M. R. 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. Internationale Revue des gesamten Hydrobiologie, 63: 77–119.

Landry, M. R. 1983. The development of marine calanoid copepods with comment on the isochronal rule. Limnology and Oceanography, 28: 614–624.

Lee, H-W., Han, S., Ikeda, T., and Matsuishi, T. 2003. Effect of temperature on development, growth and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. Journal of Plankton Research, 25: 261–271.

Lopez, M. D. G. 1991. Molting and mortality depend on age and stage in naupliar *Calanus pacificus*: implications for development of field cohorts. Marine Ecology Progress Series, 75: 79–89.

Lopez, M. D. G. 1996. Effect of starvation on development and survivorship of naupliar *Calanus pacificus* (Brodsky). Journal of Experimental Marine Biology and Ecology, 203: 133–146.

Miller, C. B., Crain, J. A., and Morgan, C. A. 2000. Oil storage variability in *Calanus finmarchicus*. ICES Journal of Marine Science, 57: 1786–1799.

Miller, C. B., Huntley, M. E., and Brooks, E. R. 1984. Post-collection molting rates of planktonic, marine copepods: measurement, applications, problems. Limnology and Oceanography, 29: 1274–1290.

Miller, C. B., Johnson, J. K., and Heinle, D. R. 1977. Growth rules in the marine copepod genus *Acartia*. Limnology and Oceanography, 22: 326–335.

Miller, C. B., Lynch, D. R., Carlotti, F., Gentleman, W., and Lewis, C. V. W. 1998. Coupling of an individual-based dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region. Fisheries Oceanography, 7: 219–234.

Niehoff, B. 2000. Effect of starvation on the reproductive potential of *Calanus finmarchicus*. ICES Journal of Marine Science, 57: 1764–1772.

Paschke, K. A., Gebauer, P., Buchholz, F., and Anger, K. 2004. Seasonal variation in starvation resistance of early larval North Sea shrimp *Crangon crangon* (Decapoda: Crangonidae). Marine Ecology Progress Series, 279: 183–191.

Peña, M. A. 2003. Modelling the response of the planktonic food web to iron fertilization and warming in the NE subarctic Pacific. Progress in Oceanography, 57: 453–479.

Peterson, W. T., and Painting, S. 1990. Development rates of the copepods *Calanus australis* and *Calanoides carinatus* in the laboratory, with discussion of methods used for calculation of development time. Journal of Plankton Research, 12: 259–281.

Rey-Rassat, C., Bonnet, D., Irigoien, X., Harris, R., Head, R., and Carlotti, F. 2004. Is weight an important parameter when measuring copepod growth? Journal of Experimental Marine Biology and Ecology, 313: 19–27.

Salonen, K. 1979. A versatile method for the rapid and accurate determination of carbon by high temperature combustion. Limnology and Oceanography, 24: 177–183.

Schultze, K. 1993. Experimentelle Untersuchungen zur Lavalentwicklung von *Pandalus montagui* (Leach, 1814) (Crustacea, Decapoda, Natantia). Dissertation Naturwissenschaft, Universität Hanover, FB Biologie, 1993.

Sciandra, A. 1986. Study and modelling of development of *Euterpina acutifrons* (Copepoda, Harpacticoida). Journal of Plankton Research, 8: 1149–1162.

Speirs, D., Gurney, W., Heath, M. R., Horbelt, W., Wood, S. N., and de Cuevas, B. A. 2006. Ocean-scale modeling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. Marine Ecology Progress Series, 313: 173–192.

Staton, J. L., and Sulkin, S. D. 1991. Nutritional requirements and starvation resistance in larvae of the brachyuran crabs *Sesarma cinereum* (Bosc) and *S. reticulatum* (Say). Journal of Experimental Marine Biology and Ecology, 152: 271–284.

Steele, J. H. 1998. Incorporating the microbial loop in a simple plankton model. Proceedings of the Royal Society of London, Series B, 265: 1771–1777.

Steele, J. H., and Clark, G. W. 1998. Relationships between individual- and population-based plankton models. Journal of Plankton Research, 20: 1403–1415.

Tsuda, A. 1994. Starvation tolerance of a planktonic marine copepod *Pseudocalanus newmani* Frost. Journal of Experimental Marine Biology and Ecology, 181: 81–89.

Uye, S., Iwai, Y., and Kasahara, S. 1983. Growth and production of the inshore marine copepod *Pseudodiaptomus marinus* in the central part of the Inland Sea of Japan. Marine Biology, 73: 91–98.

van den Bosch, F., and Gabriel, W. 1994. A model of growth and development in copepods. Limnology Oceanography, 39: 1528–1543.

Vidal, J. 1980a. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Marine Biology, 56: 111–134.

Vidal, J. 1980b. Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* sp. Marine Biology, 56: 135–146.

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