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Differential dormancy of co-occurring copepods

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Abstract

Four species of planktonic calanoid copepods that co-occur in the California Current System (*Eucalanus californicus* Johnson, *Rhincalanus nasutus* Giesbrecht, *Calanus pacificus californicus* Brodsky, and *Metridia pacifica* Brodsky) were investigated for evidence of seasonal dormancy in the San Diego Trough. Indices used to differentiate actively growing from dormant animals included developmental stage structure and vertical distribution; activity of aerobic metabolic enzymes (Citrate Synthase and the Electron Transfer System complex); investment in depot lipids (wax esters and triacylglycerols); in situ grazing activity from gut fluorescence; and egg production rates in simulated in situ conditions. None of the 4 species exhibited a canonical calanoid pattern of winter dormancy – i.e., synchronous developmental arrest as copepodid stage V, descent into deep waters, reduced metabolism, and lack of winter reproduction. Instead, *Calanus pacificus californicus* has a biphasic life history in this region, with an actively reproducing segment of the population in surface waters overlying a deep dormant segment in winter. *Eucalanus californicus* is dormant as both adult females and copepodid V's, although winter females respond relatively rapidly to elevated food and temperature conditions; they begin feeding and producing eggs within 2–3 days. *Rhincalanus nasutus* appears to enter dormancy as adult females, although the evidence is equivocal. *Metridia pacifica* shows no evidence of dormancy, with sustained active feeding, diel vertical migration behavior, and elevated activity of metabolic enzymes in December as well as in June. The four species also differ markedly in water content, classes of storage lipids, and specific activity of Citrate Synthase.

These results suggest that copepod dormancy traits and structural composition reflect diverse adaptations to regional environmental conditions rather than a uniform, canonical series of traits that remain invariant among taxa and fixed across a species' range. Such

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interspecific and regional differences in life history traits need to be incorporated in models simulating Eastern Boundary Current pelagic ecosystem dynamics. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

Dormancy is an important life history trait of many species of copepods and other planktonic organisms. Seasonal intervals of dormancy in subsurface waters can confer several adaptive advantages on planktonic populations (Dahms, 1995; Hirche, 1996), including predator avoidance during intervals of high predation risk in near-surface waters (Hairston, 1987; Kaartvedt, 1996). Immobility and quiescence at depth also may reduce encounter rates with mechanosensory-hunting predators (Hirche, 1996). In regions with seasonal production cycles, dormant animals can minimize starvation losses by avoiding surface waters at times of low food availability. For species with multi-year life histories, partial-year residence in deep waters can result in larger adult body size and, consequently, increased fecundity in a subsequent growing season (McLaren, 1966). Another possible benefit of dormancy is the synchronization of life history events, for example where the short-lived males of amphiscandrid calanoid copepods may have more predictable fertilization success if newly molted females emerge from dormancy at predictable times of year. In regions with strong vertical current shear, increased time in deep waters during dormant periods may increase animals' residence time in favorable habitats (e.g. Eiane et al., 1998). Dahms (1995) reports other potential adaptive advantages of dormancy.

Dormancy must be understood and properly described mathematically in models simulating the dynamics of populations and pelagic ecosystems. Dormant animals define the "initial conditions" for seasonal population growth which, in nature, may be important determinants of population size and grazing pressure later in the season (Carlotti and Radach, 1996). Deterministic models are typically sensitive to choice of initial conditions used for initialization. The manner in which dormancy is treated is important to the structure of such models because assumptions about dormancy influence the time scales of the processes controlling population growth and reproduction. When dormancy is ignored, zooplankton abundance, body mass, rate of somatic growth, and reproduction are typically described as instantaneous functions of current conditions in the water column. However, where dormancy occurs, time lags must be considered. The abundance, body size, and lipid content of the animals emerging to initialize population growth may have been established several months previously in an earlier growing season, thus shifting both the time scale and processes governing entry to a population.

The textbook or "canonical" dormancy response thought to characterize many members of the family Calanidae includes seasonal accumulation of subadult stages (commonly copepodid stage V), sustained day/night residence in deeper strata over the winter period, arrested development, reduced metabolic rates, cessation of feeding, and lack of winter reproduction. Many variations on this theme have been reported

and, increasingly, departures from this idealized description have been recognized (Conover, 1988; Pedersen et al., 1995; Hirche, 1996).

Calanus pacificus exemplifies some of the variability in dormancy responses that may be seen in different parts of a species' range. Brodsky (1965) recognized the separate subspecies *C.p. californicus* from the NE Pacific off the shores of North America. Recent evidence based on the analysis of mitochondrial DNA sequence variations is in agreement with the differentiation of the subspecies *C.p. californicus* from the oceanic subarctic Pacific subspecies *C.p. oceanicus* (Bucklin et al., 1995). *C.p. californicus* has been reported from the California Current System and nearby coastal waters, ranging from ca. 48°N off Vancouver Island and Puget Sound (Brodsky, 1965; Bucklin and LaJeunesse, 1994) to 23°N in the Gulf of California (Fleminger, 1964; Brinton et al., 1986).

A temperate-boreal population of *C. pacificus* in Dabob Bay (ca. 47°45'N)—that we take to be the subspecies *californicus* based on collection localities reported in Bucklin and LaJeunesse (1994)—exhibits the canonical dormancy response. Copepodid V's accumulate and dominate the stage structure of the population during autumn–winter, most of which remain in deeper water day and night in October and February (Osgood and Frost, 1994). Egg production by females does not begin in this locality until March. However, at lower latitudes, *C. pacificus* shows a rather puzzling combination of life history characteristics. Deep layers of *C. pacificus*, composed mainly of copepodid stage V's that have been interpreted as dormant animals, have been sampled in the Southern California Bight (Santa Barbara Basin—Alldredge et al., 1984; Osgood and Checkley, 1997; San Diego Trough—present study) and further south off Baja California (Longhurst, 1967; Alldredge et al., 1984). However, contrasting with these studies, Mullin and Brooks (1967) documented the continuous, year-round presence of nauplii of *C. pacificus* in the upper 90 m in the La Jolla Bight. The year-round availability of adult female *C. pacificus* in near-surface waters in this locality continues to the present day (pers. observ.). Extensive egg production experiments have shown that *C. pacificus* sustains egg production throughout the year in the S. California Bight (Mullin, 1991, 1993), although there is considerable spatial variability. These results suggest continuous reproduction and population growth rather than a seasonally interrupted life history punctuated by an interval of dormancy. Hence, there is an apparent paradox: characteristics of this species in the Southern California Bight region are consistent with seasonal dormancy on the one hand and with continuous recruitment on the other. This uncertainty regarding discontinuous or continuous population growth influences the ability to successfully model and predict population growth of one of the dominant species of zooplankton in the California Current System.

Calanus pacificus californicus, endemic to the California Current System, co-occurs with many other copepod species over a geographically extensive region of the NE Pacific. In addition to the need to resolve the apparent contradictions in the life history of *C.p. californicus*, it is of considerable interest to determine the extent to which co-occurring species share life history traits. Does the joint occurrence of *C.p. californicus* with *Eucalanus californicus*—a more broadly distributed Transition Zone species (Fleminger, 1973; Fleminger and Hulsemann, 1973)—imply common timing of

dormancy and reproductive responses? Does the co-occurrence of these two species with *Rhincalanus nasutus*, a cosmopolitan species (Lang, 1965; Hauray, 1984) and *Metridia pacifica*, a Transition Zone-Boreal species (Hauray, 1984; Batchelder, 1985)—imply common or divergent life history traits?

The term “dormancy” encompasses both true diapause and quiescence (see Dahms, 1995). Diapause *sensu stricto* implies genetically determined, obligate arrested development and growth, that occurs at predictable developmental stages and may be induced by various environmental stimuli (Dahms, 1995). Diapause is under endocrine control (Hirche, 1996). Quiescence involves arrested development in direct response to adverse conditions, need not occur at fixed developmental stages, and may occur repeatedly in the same individual. It is rarely possible to differentiate diapause and quiescence in field studies. We therefore prefer the more general, inclusive term dormancy which makes no assumptions about underlying control mechanisms.

Dormancy is not readily assessed by a single type of measurement, because most components of copepod dormancy—altered development, growth, feeding, metabolism, and reproduction—differ not only between active and resting animals, but also vary in response to environmental variations in food supply and temperature. Hence, we rely on several measures that, taken together, permit us to assess the state of activity of the animals. We emphasize the state of the animals in winter (here, December) as the most likely time period to detect dormant animals. Under the hypothesis of winter dormancy, if animals were to follow a “canonical” calanoid response the following describes the expected state of each measure.

Diel vertical migration behavior: Dormant animals remain in deep strata and show no diel changes in vertical distribution.

Developmental stage structure: Dormant populations are dominated by late copepodid stages (generally CV), with no adult females present.

Reproduction: Adult females are generally not present, but if they are present and dormant, they are not capable of releasing eggs in short-term incubations.

Lipid reserves: Dormant animals have high investment in wax esters (typically considered long-term reserve lipids, e.g. Håkanson, 1984).

Lipid mobilization: Storage lipids are not mobilized, or only very slowly, upon starvation.

Aerobic metabolism: Metabolic rates of dormant animals are reduced in comparison with actively feeding and growing animals.

Grazing: Dormant animals show no grazing activity.

Most of the above measurements are well known, but our assessment of metabolic rates requires further explanation. We assessed the aerobic metabolic potential of copepods from the activity of metabolic enzymes. Assay of enzyme activity may be preferred over incubation methods for assessing metabolic rates because enzymatic assays avoid the artifacts associated with collecting, handling, and incubating planktonic animals for rate determinations. These problems can become particularly severe with animals collected from mesopelagic or deeper depths. Here we assessed aerobic metabolic potential from two independent enzyme assays. One is Citrate Synthase (CS), a principal regulatory enzyme of the Krebs cycle. CS activity is correlated with

Fig. 1. Adult female copepods from the California Current System, in dorsal view. All are drawn to scale.

oxygen consumption rate in many species of fish (Torres and Somero, 1988), pelagic worms (Thuesen and Childress, 1993a), chaetognaths (Thuesen and Childress, 1993b), and, to a lesser extent, medusae (Thuesen and Childress, 1994). The second is the Electron Transfer System (ETS) assay, which measures the activity of a complex of dehydrogenase enzymes (NADH, NADPH, and succinate dehydrogenase) involved in both mitochondrial and microsomal electron transfer (Owens and King, 1975; Mayzaud, 1986). NADH and NADPH dehydrogenases generally account for most of the activity measured in the ETS assay (Savenkoff et al., 1995). Although the ratio of ETS activity to respiration rate for copepods has been reported to vary between 0.3 and 6 (Båmstedt, 1980; Mayzaud, 1986), the ratio for relatively unstressed copepods is typically 1.9–2.2 (Owens and King, 1975; Flint et al., 1991; Pasternak et al., 1994; Arashkevich et al., 1996), and thus this assay generally correlates with oxidative metabolic rate. The assays for both CS and ETS measure maximum enzyme activity when provided saturating concentrations of substrates and therefore represent potential aerobic metabolism, not necessarily corresponding to the rate of enzyme activity in the field (Hochachka and Somero, 1984).

The four species of copepods analyzed differ in size (Fig. 1) and it is therefore necessary to scale metabolic relations and lipid content to make valid interspecific comparisons of dormancy characteristics. To test the assumption that all four copepod species show common structural composition and are thus being scaled with an appropriate “currency”, we compared the relationship between mass, water, lipid, and protein content among species.

2. Materials and methods

Sampling was carried out in the San Diego Trough (near 32° 50'N, 117°40'W) on cruises ZB2 (6–14 June 1992) and ZB4 (15–22 December 1992) while tracking a holey sock drifter (Niiler et al., 1995) drogued at 15 m depth. Zooplankton were sampled with a 20-net, 1 m² MOCNESS (Wiebe et al., 1985), 333 µm mesh, towed at

0.75 m s^{-1} . Four MOCNESS profiles were made in the San Diego Trough in June (3 to at least 400 m depth and 1 to 135 m), and 8 profiles were made (to at least 500 m) in December. Sampling was centered around noon and midnight. Supplemental samples for enzyme and other assays were obtained with a paired vertical closing net, 0.71 m diameter, 333 μm mesh (Brown and Honegger, 1978). Supplemental “deep” samples were retrieved from 400–200 m in December and “surface” samples from 70–0 m in June or 50–0 m in December. Zooplankton were quickly frozen in liquid nitrogen for biochemical assays after draining excess water, or were preserved in 3.7% formaldehyde for enumeration. Copepods were enumerated from several replicate aliquots obtained with a Stempel pipette.

2.1. Metabolic enzymes

For assay of citrate synthase (EC 4.1.3.7) activity, individual copepods were sorted from frozen samples into 50 mM Hepes buffer, pH 7.5, sonicated in an ice bath, centrifuged, and the activity in the supernatant measured at 24°C (Clarke and Walsh, 1993). Absorbance at 412 nm was measured kinetically on a multi-well plate reader. Enzyme activity was obtained from the slope of the reaction rate, where 1 unit of CS activity = 1 μmol of substrate converted to product min^{-1} . Ten to 33 individuals were assayed per stage/species/depth treatment, except for shallow *E. californicus* females in December ($N = 1$).

In experiments preparatory to the measurement of Electron Transfer System (ETS) activity we found that thawed whole copepods lost ETS activity rapidly (0.8% activity lost min^{-1}), even when maintained below 4°C. This concurs with Båmstedt's (1980) result that cell-free homogenates at 2°C lost about half their ETS activity within 24 h. Hence, copepods were thawed, sorted, and extracted quickly (within 5–10 minutes). For ETS assays, lots of 3–6 copepods (5–10 in the case of *M. pacifica*) of a single developmental stage were extracted in ice cold ETS solution B (Owens and King, 1975) by sonication. Following centrifugation, the supernatant was assayed for activity of (ETS) enzymes (Owens and King, 1975) at 15°C as well as for total protein content by the BCA method (Smith et al., 1985) using bovine serum albumin in ETS B solution as a standard. ETS activity has commonly been reported in units of equivalent oxygen consumption time $^{-1}$ ($\mu\text{l O}_2$ copepod $^{-1} \text{ h}^{-1}$; cf. Owens and King, 1975; Arashkevich et al., 1996) and the values reported here are equivalent to such previous numbers. However, as we have not established the correspondence between actual oxygen consumption rates for our experimental animals and the potential rates inferred by the assay, we report these values as ETS “activity copepod $^{-1}$ ” rather than using the conventional units. Sample sizes were 4–16 replicate extractions per stage/species/depth treatment for both ETS and protein measurements.

The temperature sensitivity of ETS activity was assessed by homogenizing lots of 12–16 copepods in ETS B and centrifuging, as above, then incubating three aliquots of the supernatant at a series of temperatures. We calculated Q_{10} 's from the rates measured at the minimum and maximum assay temperatures using the formula in Prosser (1991).

2.2. Lipids

Lipids from lots of 4–8 copepods (8–12 *M. pacifica*) were extracted in 2:1 chloroform:methanol and analyzed by TLC-FID according to Ohman (1997). Sample sizes were 5–10 replicate extractions per treatment. Standard compounds used for TLC-FID calibration were native wax esters purified from *C. pacificus* and tripalmitin, myristic acid, cholesterol, and L- α -phosphatidylcholine from Sigma Biochemical Co. Recent work with TLC-FID for the analysis of copepod lipids (Miller and Morgan, 1996; Ohman, 1997) shows the necessity of calibration with wax esters extracted from the animals of interest rather than wax esters purchased commercially. The small quantity of free fatty acids in all species illustrates the lack of lipid degradation and confirms the suitability of the collection, freezing, and extraction procedures (cf. Ohman, 1996).

Lipid utilization during starvation was analyzed in *E. californicus* females in shipboard experiments in December (cruise ZB4). Animals were collected with a 1 m diameter, 333 μ m mesh net with large cod end reservoir in an oblique haul to a depth of 350 m. Within 1–4 h of capture, groups of 20 females were placed in 2 L polycarbonate containers of glass fiber (GF/F) filtered seawater maintained in the dark at either 8°C (temperature at 300 m) or at 15°C (mixed layer temperature) during the starvation experiments. At daily intervals a group of copepods was frozen in liquid N₂. In the laboratory, females were sorted into lots of 4–6 ($N = 2$ –5 replicate extractions per time point), lipids extracted, and analyzed for lipid class composition by TLC-FID.

2.3. Water content

Wet mass of individual copepods was measured on a Cahn 29 electrobalance, animals dried at 55°C, then dry mass measured and water content determined by difference (details in Ohman, 1997). Only adult females ($N = 20$ –33 per species) were used for these analyses, with all females collected in winter except *Calanus* which were collected in summer. Mass, lipid, and protein content were measured on separate lots of animals from the same field samples. The approximate 95% confidence limits of the ratios of these quantities were obtained from twice the standard error of the ratio, where this standard error is calculated as detailed in Ohman et al. (1989, Eq. (1)). The same statistical procedure was used for confidence limits of ratios of other quantities that were measured on different groups of animals.

2.4. Egg production rates

Shipboard egg production experiments assessed the reproductive activity of adult female copepods collected in December. Experiments were done only with *E. californicus* (prosoma length = 5.46 ± 0.06 mm, $\bar{x} \pm 95\%$, $N = 68$ animals incubated) collected from deep waters and *C.p. californicus* (prosoma length 2.38 ± 0.02 mm, $N = 91$) collected from surface waters. Collections were made with a 1 m, 333 μ m net with a large cod end reservoir between 1500 and 2030 local time and egg production

incubations begun within 1–3 h of collection. Females were sorted individually ($N = 16$ –20 per treatment) into petri dishes containing 30 mL of seawater. Food was replenished at 12 h intervals. Females were incubated in the temperature (8° or 15°C) and ambient seawater conditions whence they originated and, in reciprocal transplant experiments, in the temperature and food conditions they would have experienced had they occurred either deeper (*C.p. californicus*) or shallower (*E. californicus*) in the water column. In all cases, ambient suspended particulate matter (SPM; collected from either 250 m or from the depth of the near-surface maximum of in vivo fluorescence) also was supplemented with a mixture of diatoms (*Thalassiosira weissflogii ad libitum*) in a separate treatment. Egg production rates were measured by counting eggs after incubation for 24 h in the dark in a temperature-controlled incubator, as a measure of in situ reproductive potential. One incubation with *E. californicus* was carried out for 5 d to assess the time course of response to enriched food.

2.5. In situ grazing

In situ grazing activity was assessed by analysis of copepod gut fluorescence. Animals were collected from 70–0 m in June and from 50–0 m and 400–200 m in December, immediately frozen in liquid nitrogen, and later sorted and homogenized in 90% acetone with an ultrasonicator. After centrifugation, the fluorescence of the supernatant was analyzed on a calibrated Turner Designs model 10 fluorometer, before and after acidification. Chlorophyll *a* and phaeopigments were summed and corrected for background tissue fluorescence from starved copepods. No adjustment was made for possible pigment destruction within copepod guts.

3. Results

3.1. Organic composition

The four copepod species differed appreciably in organic composition. While the water content of adult females of three species (*Rhincalanus nasutus*, *Calanus pacificus californicus*, *Metridia pacifica*) was 82–84% of total wet mass, the water content of female *Eucalanus californicus* averaged 93% (Fig. 2A). In life, *E. californicus* are nearly transparent with limited body musculature and a gelatinous appearance, in contrast with the other species. The appreciably higher water content of *E. californicus* females led to a lower protein content per unit wet mass (Fig. 2B). *R. nasutus* also had lower protein per unit wet mass in comparison with the remaining two species (Fig. 2B). Both *R. nasutus* and *E. californicus* had a lower protein content per unit dry mass (Fig. 2C), reflecting structural differences among species even when water is eliminated. *R. nasutus* females also had substantially higher lipid content as a fraction of total dry mass than the other three species (Fig. 2D). These interspecific differences suggest that contrasts among species will be quite sensitive to the mass units used for scaling purposes.

Fig. 2. Water content and organic composition of adult female copepods from the California Current System (*Eucalanus californicus*, *Rhincalanus nasutus*, *Calanus pacificus californicus*, and *Metridia pacifica*). (A) Water content as % of wet mass ($\bar{x} \pm 95\%$), (B) Protein content as % of wet mass ($\bar{x} \pm 2\text{S.E.}$), (C) Protein content as % of dry mass ($\bar{x} \pm 2\text{S.E.}$), (D) Lipid content as % of dry mass ($\bar{x} \pm 2\text{S.E.}$). (Confidence limits for ratios of two quantities measured on different individuals were approximated as 2S.E.; see Methods).

The lipid class composition of copepodid stage V's, the usual dormant developmental stage in marine calanoid copepods, was dominated by wax esters in *R. nasutus*, *C.p. californicus*, and *M. pacifica* (Fig. 3), but by triacylglycerols in *E. californicus*. Copepodid V's of *M. pacifica* were not generally included in subsequent analyses because of concerns about quantitative sampling of these smaller bodied animals with a 333 μm mesh net. Quantitative differences in lipid content with depth and time of year are reported below.

3.2. Vertical distribution/stage structure

In June, copepodid stage V's and adult females of *E. californicus* (Fig. 4A) were located in the upper 50 m both day and night. In December, CV's were concentrated between 250 and 400 m but extended to the deepest stratum sampled (750–800 m), with no evident difference day and night. Female *E. californicus* were also concentrated in a layer between 200 and 300 m both day and night in December, but did not extend deeper than 450 m. A very small number of *E. californicus* CV's and females was found in the upper 50 m both day and night in December.

Fig. 3. Chromatograms illustrating lipid class composition of copepodid V of *Eucalanus californicus*, *Rhincalanus nasutus*, *Calanus pacificus californicus*, and *Metridia pacifica* from the California Current System. (WE = wax esters, TAG = triacylglycerols, FFA = free fatty acids, ST = sterols, PL = polar lipids). Ordinate is scaled arbitrarily to illustrate the relative size of WE and TAG peaks for each species. PL peaks usually extend off-scale.

The distribution of *R. nasutus* (Fig. 4B) was similar to that of *E. californicus* in both June and December, except that a somewhat larger secondary mode of CV's and females occurred close to the surface in December. There was no evidence of a deep-penetrating layer of *R. nasutus* CV's, unlike *E. californicus* CV's.

Calanus pacificus californicus CV's were nearly all in the upper 50 m in June, and nearly all between 300–400 m in December (Fig. 4C). A very small secondary group of

Fig. 4. Vertical distribution of copepods in the San Diego Trough in June and December. Adult female and copepodid stage V (A) *Eucalanus californicus*, (B) *Rhincalanus nasutus*, (C) *Calanus pacificus californicus*, and (D) *Metridia pacifica* (adult females only). Dark symbols illustrate nighttime distributions, open symbols illustrate daytime distributions, each plotted at the mid-point of the sampling interval. Sampling extended deeper in December than in June.

CV's was found deeper in the water column in June and a small number of CV's were shallower in December. Adult females of *C.p. californicus* were concentrated in the upper 50 m both day and night in June. In December, the primary mode of adult females was also in the upper 25–50 m, though a secondary mode occurred in a layer between 250 and 350 m. This deeper group overlapped the layer of *C. pacificus californicus* CV, from which they are presumed to have developed.

Metridia pacifica females showed strong diel vertical migrations from 250 to 350 m by day to the upper 50 m by night (Fig. 4D). This behavior occurred equally in December and June, with no evidence of secondary population modes in any of the vertical series. Notably, all adult female *M. pacifica* underwent this diel vertical migration. None of the other three species analyzed showed any evidence of DVM in either June or December.

Table 1

Ratio of copepodid stage V to adult female abundance ($\bar{x} \pm 95\%$), summed over the water column in the San Diego Trough

Month	<i>Eucalanus californicus</i>	<i>Rhincalanus nasutus</i>	<i>Calanus pacificus californicus</i>	<i>Metridia pacifica</i>
June (<i>N</i> = 7–8)	0.54 $\pm$ 0.58	0.24 $\pm$ 0.20	0.54 $\pm$ 0.90	0.49 $\pm$ 0.96
December (<i>N</i> = 3)	2.25 $\pm$ 0.50	0.13 $\pm$ 0.02	69.75 $\pm$ 26.13	1.32 $\pm$ 1.13

The ratio of copepodid stage V to adult females can provide an indirect measure of dormancy. If animals enter dormancy as CV's, the CV:female ratio should increase markedly. Such a pattern was observed for *C. pacificus californicus* ($P < 0.05$, Table 1), and the ratio increased slightly for *E. californicus* but not significantly for *R. nasutus* or *M. pacifica*. Although escapement of *M. pacifica* CV's from the net may bias the CV:female ratio for this species, we do not expect the bias to differ between June and December.

3.3. Storage lipids

Lipids of copepodid stage V's and adult females were analyzed from the modal population layers in June and December, whenever sufficient animals were available. These analyses focused on storage compounds (wax esters, triacylglycerols), although the analytical method resolved other lipid classes as well. In all cases, *E. californicus* CV's and females contained very little wax ester (Fig. 5A). The primary depot lipid in both developmental stages was triacylglycerol (TAG; Fig. 5B). The TAG content of both adult females and CV's was high at depth in December. The deep *E. californicus* females had over 2X the TAG content of surface-dwelling females in June and 5X that of the small mode of surface-dwelling females in December. The occurrence of high triacylglycerol content in animals living far away from the surface was rather surprising, in light of the common view that such lipids are short-term energy reserve compounds that are metabolized quickly upon starvation. If TAGs are utilized as short-term reserves by *E. californicus*, this would imply that the deep-dwelling animals are actively feeding and not in a dormant state.

We tested the time course of depletion of TAG's by *E. californicus* in short-term shipboard starvation experiments in December. Adult females recovered from 0 to 350 m depth were incubated for 5 d at 8°C (ambient temperature at depth) or for 2 d at 15°C (the near-surface temperature; insufficient animals were collected to extend these incubations longer). In neither experiment was a temporal trend in TAG content detectable (Fig. 6). There was no evidence for utilization of TAGs by adult female *E. californicus* over the time period of these experiments.

Fig. 5. Lipid composition of *Eucalanus californicus* (Ec), *Rhincalanus nasutus* (Rn), *Calanus pacificus californicus* (Cp), and *Metridia pacifica* (Mp) from the San Diego Trough. Variation with depth and time of year. 5 = copepodid stage V, ♀ = adult females. (A) Wax esters, (B) Triacylglycerols, (C) Total lipid, (D) Sterols, (E) Polar lipids. Where bars are missing, insufficient animals were available for analysis. ($\bar{x} \pm 95\%$).

Rhincalanus nasutus females were characterized by very high wax ester content both at the surface in June and in deep water in December (Fig. 5A). The small mode of females at the surface in December had significantly lower wax ester content than the deeper dwelling females at the same time of year. CVs of *R. nasutus* were not analyzed.

Calanus pacificus californicus CVs showed a substantial accumulation of wax esters from $12.6 \mu\text{g copepod}^{-1}$ near surface in June to $84.3 \mu\text{g copepod}^{-1}$ in deep water in December (Fig. 5A). This accumulation is consistent with the “canonical” dormancy response for members of the *Calanidae*. *C.p. californicus* adult females had negligible

Fig. 6. Response of triacylglycerol content of *Eucalanus californicus* females to starvation, at (A) 8°C and (B) 15°C ($\bar{x} \pm \text{S.E.}$). *E. californicus* collected between 0–350 m in December.

wax esters when near the surface in June and significantly higher wax ester content near the surface in December. Notably, the small, secondary population mode of adult females at 300–400 m in December (Fig. 4) had appreciably higher wax ester content than the surface females (Fig. 5A). Their wax ester (WE) content was 59% of that of co-occurring CVs of *C.p. californicus*. In contrast to wax esters, the TAG content of CVs and adult females was relatively low and did not differ among different collections (Fig. 5B).

Metridia pacifica adult females had relatively low wax ester and triacylglycerol content, neither of which differed between June and December (Fig. 5).

The sterol content of copepods (Fig. 5D) was found to vary with copepod size, measured as protein content. Taken across all species/stage combinations, sterol content was significantly correlated with protein content (Spearman's $\rho = 0.763$, $P < 0.01$, $N = 15$). This result is consistent with the primary structural role of sterols as components of membranes and myelin sheaths. Although polar lipids (chiefly phospholipids, Fig. 5E) also varied with body size, the correlation was somewhat weaker ($\rho = 0.671$, $P < 0.01$, $N = 15$). Because sterol content varies with body size and, unlike protein, was measured from the identical animals as the depot lipids, sterols were useful for scaling the storage lipid content of copepods of different body size. Comparison of the WE and TAG content per copepod in Fig. 5A and B with values scaled per unit sterol content in Fig. 7A and B reveals similar trends, but the scaled values have the advantage that they correct for differences that may be attributable to size alone. The ratio WE:ST is an appropriate measure for *R. nasutus*, *C.p. californicus*, and *M. pacifica*, all of which store primarily wax esters, while the ratio TAG:ST is more appropriate for *E. californicus*.

3.4. Metabolic enzymes

The citrate synthase activity of *E. californicus* diminished in deep water in December in comparison with surface waters in June. Though this decrease was significant for adult females ($P < 0.05$), it was not for CV's ($P > 0.05$, Fig. 8A). The protein-specific CS activity, which adjusts for differences in body size, showed a more

Fig. 7. Ratio of (A) wax esters:sterols (WE:ST) and (B) triacylglycerols:sterols (TAG:ST). Variation with depth and time of year. Abbreviations as in Fig. 5 legend. ($\bar{x} \pm 95\%$).

pronounced decrease (Fig. 8B). This diminution in enzyme activity, together with vertical distribution and lack of mobilization of lipids upon starvation, suggests winter dormancy of both CV and adult female *E. californicus*.

In *R. nasutus*, there was no significant difference between CS activity per copepod in June surface and December deep animals (Fig. 8A). When adjusted for the difference in protein content, there was a small decrease in CS activity ($P < 0.05$).

For *C.p. californicus* CV, the CS activity declined 4.5-fold between June in surface waters and December in deep waters. When corrected for differences in protein content this became a 6.1-fold decline. This decline, together with other evidence presented, is consistent with dormant CVs at depth. The CS activity of adult female *C.p. californicus* was 5.1-fold higher in June at the surface than in December at depth. On a protein-specific basis, the difference was only 2.8-fold. Females at depth had slightly higher protein-specific activity than CVs at depth while surface females had much higher (4.3-fold) protein-specific activity than deep CVs.

Metridia pacifica females had comparable CS activity in June and December.

When considering each species individually, electron transfer system (ETS) activity showed very similar trends as CS activity. For example, protein-specific ETS and CS activity in deep *C.p. californicus* females was about twice as high as that of deep CVs and no different ($P > 0.05$) than that of winter surface females. However, a surprising difference emerged in comparisons among species. Although the ETS activity of *C.p. californicus* was comparable to (or higher than) the other three species (Fig. 8C), the CS activity of *C.p. californicus* was lower than the CS activity of the other three species. This contrast is particularly apparent in the protein-specific activities (Fig. 8B vs. D). These data are replotted in Fig. 9 to illustrate the contrast between enzymes. CS activities of *C.p. californicus* were consistently lower than those of the other species, regardless of depth, developmental stage, time of year, or occurrence of dormancy. The same contrast among species is seen as when expressed as rates per individual.

Fig. 8. Activity of metabolic enzymes and copepod protein content. Variation with depth and time of year. (A) CS (Citrate Synthase) activity copepod⁻¹ ($\bar{x} \pm 95\%$), (B) CS activity protein⁻¹ ($\bar{x} \pm 2$ S.E.), (C) ETS (Electron Transfer System) activity copepod⁻¹ ($\bar{x} \pm 95\%$), (D) ETS activity protein⁻¹ ($\bar{x} \pm 95\%$). (E) Protein content copepod⁻¹ ($\bar{x} \pm 95\%$). CS assayed at 24°C, ETS at 15°C. Abbreviations as in Fig. 5 legend. (Confidence limits for ratios of two quantities measured on different individuals approximated as 2 S.E.; see Methods).

CS activity has a greater range of variation than ETS activity. On a protein-specific basis CS activity varied 25.1-fold, from lowest to highest mean (Fig. 9), while ETS activity varied 3.4-fold. Part of this difference arises from the correlation of ETS activity with protein content ($\rho = 0.609$, $P < 0.02$, $N = 15$), suggesting that some (but not all) of the difference between species in ETS activity is caused only by differences in body mass and hence in mass of respiratory tissue. In contrast, CS activity, was

Fig. 9. Relationship between protein-specific activity of the metabolic enzymes Citrate Synthase and the Electron Transfer System complex. Filled symbols are all *Calanus pacificus californicus* ("C"); other symbols are *Eucalanus californicus* ("E"), *Rhincalanus nasutus* ("R"), and *Metridia pacifica* ("M"), where "S" = copepod stage V, otherwise adult females; J = June surface collection, D = December surface, DD = December deep. Bivariate confidence limits illustrate $\bar{x} \pm 95\%$ for ETS/protein and $\bar{x} \pm 2\text{S.E.}$ for CS/protein.

uncorrelated with copepod protein content ($\rho = 0.050$, $P > 0.20$, $N = 15$). With the greater dynamic range of CS activity and independence from copepod body size, CS appears to be a more sensitive indicator than ETS of changes in metabolic potential.

The temperature sensitivity of ETS was measured to correct enzyme activities to in situ temperatures. The Q_{10} 's for ETS activity ranged from 2.06 to 2.54, mean $\pm$ S.D. = 2.31 ± 0.19 (Fig. 10A). These same Q_{10} 's were applied to CS activity. For *E. californicus* CV and adult females corrected to in situ temperatures, the deep winter animals had 3–4 fold lower metabolic enzyme activities than the near-surface animals in June (Fig. 10B and C). *R. nasutus* females had 2-fold lower activities in December. *C.p. californicus* CV showed a 4 to 11-fold reduction in temperature-corrected activity. Deep-dwelling adult female *C.p. californicus* in December showed a 2 to 5-fold reduction in activity in comparison with females in June. Notably, the surface-dwelling females in December showed no significant difference in metabolic potential from surface-dwelling females in June. For *M. pacifica* females, temperature-corrected activities of both metabolic enzymes were no different in June than December.

3.5. In situ Grazing

Gut fluorescence analysis showed that *C.p. californicus* and *M. pacifica* females were actively ingesting phytoplankton in surface waters in both June and in December

Fig. 10. (A) Temperature-sensitivity of ETS activity. Numerals to the left of each species designation indicate the Q_{10} calculated from the adjoining data. *Cp* = *Calanus pacificus californicus* (circles), *Rn* = *Rhincalanus nasutus* (diamonds), *Ec* = *Eucalanus californicus* (squares). *Mp* = *Metridia pacifica* (triangles). Adult females (open symbols) or copepodid stage V (filled). Variation with depth and time of year of protein-specific activity of (B) CS and (C) ETS, corrected to ambient temperature (15 $^{\circ}$ C near surface in June and December; 8 $^{\circ}$ C at depth in December). Abbreviations as in Fig. 5 legend.

(Table 2). (Grazing activity of *E. californicus* and *R. nasutus* was not assessed in June.) None of the species or stages analyzed from deep waters in December (*E. californicus* CV and females, *R. nasutus* females, *C.p. californicus* CV and females) showed gut fluorescence that differed significantly from detection limits.

3.6. Egg production

Eucalanus californicus females released no eggs in either simulated in situ conditions (8 $^{\circ}$ C, deep SPM) or in the conditions they would have experienced had they been transported to near-surface waters (15 $^{\circ}$ C, fluorescence maximum SPM; Fig. 11).

Table 2

In situ gut fluorescence (ng pigment copepod⁻¹, $\bar{x} \pm 95\%$, (N)) in the San Diego Trough. — indicates no copepods were analyzed. All of the analyses from deep water in December were at the limit of analytical resolution and did not differ from 0

	June (near surface)	December (near surface)	December (200–400 m)
<i>Eucalanus californicus</i> —female	—	—	0.05 $\pm$ 0.05 (21)
<i>E. californicus</i> —CV	—	—	0.18 $\pm$ 0.30 (29)
<i>Rhincalanus nasutus</i> —female	—	—	0.03 $\pm$ 0.12 (3)
<i>Calanus pacificus californicus</i> —female	6.43 $\pm$ 1.42 (73)	5.07 $\pm$ 0.45 (132)	0.20 $\pm$ 0.55 (5)
<i>C. pacificus californicus</i> —CV	—	—	0.00 $\pm$ 0.00 (32)
<i>Metridia pacifica</i> —female	3.54 $\pm$ 0.54 (67)	2.83 $\pm$ 0.19 (130)	—

In contrast, *C.p. californicus* females released substantial numbers of eggs in both treatments when incubated in ambient seawater, with about twice the number released at 15°C as at 8°C (Fig. 11). When incubated in diatom-enriched seawater, *C.p. californicus* released 2–3 times the number of eggs released in ambient seawater.

A longer-duration egg production experiment with *E. californicus* females assessed the time course of response to increased food supply at near-surface temperatures. In this experiment, appreciable numbers of eggs were released after 2.5 d in diatom-enriched seawater at 15°C (Fig. 11C), with the daily per capita egg production rate exceeding 100 after 5 days. Some fecal pellets were detected in the enriched (but not ambient seawater) treatment after as little as 1 day. These results suggest that although the female *E. californicus* collected in December were not immediately reproductively active, grazing activity and egg production were stimulated within a relatively short time upon exposure to high food levels.

3.7. Dormancy index

An index of copepod dormancy that makes use of both metabolic enzyme activity (citrate synthase) and depot lipid content can be constructed (Fig. 12). Both CS activity and depot lipids are scaled to body mass (as protein and sterol content, respectively) to permit animals of different sizes to be compared. The *E. californicus* dormancy index is based on TAG content while the other three species were based on WE content because *E. californicus* were found to store triacylglycerols while dormant. For active animals, the activity of metabolic enzymes tends to be high and depot lipid content low, while the converse is true for dormant copepods (Fig. 12). However, while this index is appropriate for *C.p. californicus*, *M. pacifica*, and *E. californicus*, it is not for *R. nasutus*. *R. nasutus* females have relatively high activity of metabolic enzymes when wax ester content is high, suggesting different lipid and enzyme regulatory mechanisms from the other three species (Table 3).

Fig. 11. Per capita egg production rate of adult female *Eucalanus californicus* and *Calanus pacificus californicus* in December. *E. californicus* females collected from the 200–350 m layer; *C. pacificus californicus* females collected in the upper 50 m (see Fig. 4B). Daily egg production rate after 24 hours incubated at: (A) 8°C in ambient seawater from 300 m (Amb) or enriched with the diatom *Thalassiosira weissflogii* (Enr). (B) 15°C in ambient seawater from the depth of the fluorescence maximum layer or enriched with *T. weissflogii*. Experiments were conducted twice. (C) Time course of egg production of *E. californicus* females upon incubation in ambient seawater from the depth of the fluorescence maximum layer or in ambient seawater enriched with *T. weissflogii*. Experiments conducted at 15°C. ($\bar{x} \pm 95\%$).

4. Discussion

4.1. Interspecific variations

These four species of copepods differ appreciably in structural composition and patterns of winter dormancy in the southern sector of the California Current System.

Fig. 12. A dormancy index based on the activity of Citrate Synthase and the storage of depot lipids. Enzyme activity and lipid mass are scaled to copepod mass (enzyme activity/protein and depot lipids/stanol). (A) *Calanus pacificus*, *Metridia pacifica*, and *Rhinocalanus nasutus*, which store primarily wax esters, and (B) *Eucalanus californicus* which stores primarily triacylglycerols. *R. nasutus* does not conform to the relationships for the other species.

None exhibits the canonical calanoid dormancy response. Despite—or perhaps because of—the geographic co-occurrence of these species in large regions of the California Current System (Fleminger, 1964; Lang, 1965; Bowman and Johnson, 1973; Haury, 1984) and elsewhere in the NE Pacific, these species respond to a common environment in different ways.

Eucalanus californicus is distinctive in many respects. The watery, gelatinous composition of its body tissues (Flint et al., 1991; Ohman, 1997) sets it apart from the other three species here and from most other calanoid copepods (cf. Båmstedt, 1986). It differs substantially even from *R. nasutus*, another member of the family Eucalanidae. The high water content, yet relatively large size of *E. californicus*, enables it to attain some of the advantages of large body size without incurring some of the associated costs. One advantage of larger body size is increased fecundity. *E. californicus* achieves higher egg production rates (Smith and Lane, 1991; present study) than *C. pacificus* (Runge, 1985; Mullin, 1991, 1994). Yet, with most of the tissue as water, the mass of respiratory tissue in *E. californicus* is lowered. While the respiratory rate of *E. californicus* tissue is equivalent to (or greater than) than that of the other three species on a protein-specific basis, when expressed per unit wet mass, the CS activity of *E. californicus* is lower than all species except *C. pacificus*. ETS activity per unit wet mass is 2.5–19 times lower than all the other species. Decreasing the amount of respiratory tissue per unit body volume should accomplish a significant metabolic savings. The larger size of *E. californicus* is unlikely to render them susceptible to visually feeding predators because the animals are remarkably transparent, with little visible muscle mass.

Table 3

Summary of evidence regarding winter dormancy, San Diego Trough. (DVM = diel vertical migration behavior; CV = copepodid stage 5; TAG = triacylglycerols; WE = wax esters.)

Species	<i>Eucalanus californicus</i>	<i>Rhincalanus nasutus</i>	<i>Calanus pacificus californicus</i>	<i>Metridia pacifica</i>
Winter dormancy	Dormant as CV and female	(Possibly) Dormant as female	Biphasic Surface active females Deep dormant CV's	No Dormancy
Vertical distribution	No DVM	No DVM	No DVM; bimodal distn. of females	Strong DVM by females
Stage structure (CV: female ratio)	2.2	0.1	69.8	1.3
Metabolic enzymes	Reduced metabolism, CV and fem	Slightly reduced metabolism	High metabolism (fem at surface); reduced metabolism (CV at depth)	High metabolism
Lipids	TAG; no depletion upon starvation	High WE	High WE (CVs)	Low lipids
In situ grazing	None at depth	None at depth	None at depth; females graze at surface	Grazing at surface
Egg production	No egg production	—	Active egg production	—

Eucalanus californicus stores mainly triacylglycerols (TAGs), rather than wax esters, as noted previously (Ohman, 1988). The starvation experiments suggest that these triacylglycerols are utilized differently by *E. californicus* than other calanoid copepods. Studies with several species have shown that TAGs are mobilized quickly upon starvation and are depleted more quickly than wax esters (Lee et al., 1971; Lee, 1974; Håkanson, 1984; Sargent et al., 1977; Sargent and Henderson, 1986; Ohman and Runge, 1994). Such results led Håkanson (1984) to characterize triacylglycerols as short-term lipids that are preferentially mobilized upon starvation, and wax esters as long-term lipids that are mobilized much more slowly. While this characterization may be accurate for many calanoid copepods, it is not for *E. californicus*. Whether the TAGs of *E. californicus* are mobilized more slowly because of unique structural characteristics of the particular fatty acids synthesized or because of different metabolic regulation of TAG catabolism during dormancy remains to be determined. *Calanus propinquus* in antarctic waters (Hagen et al., 1993) and *C. simillimus*

in subantarctic waters (Ward et al., 1996) have also been found to store mainly TAGs.

The combined evidence suggests that *E. californicus* is dormant in winter as both copepodid stage V and adult females. Both developmental stages are found in subsurface layers below 200 m in winter day and night, with relatively high depot lipids and reduced activity of metabolic enzymes. The deep winter females showed no depletion of depot lipids in short-term experiments, no evidence of in situ feeding, and no egg production. Although the *E. californicus* females show characteristics consistent with a dormant state, they are able to respond relatively rapidly to changes in their environment. The response time for detectable grazing activity, as measured by the first production of fecal pellets, was 1 d and for appreciable production of eggs was 2.5 d. In collecting animals from deep water we may have artificially stimulated them, however there was negligible egg production unless *E. californicus* females were supplemented with elevated food. Hence, we conclude that the females are probably able to respond quickly in nature when food conditions become conducive to egg production. This rapid response capability is consistent with the egg production by *E. californicus* measured by Smith and Lane (1991) in elevated food concentrations in coastal filaments much farther north in the California Current System. The likelihood that female *E. californicus* enter dormancy is consistent with a similar phenomenon inferred for *E. bungii* in the Subarctic Pacific (Miller et al., 1984).

Rhincalanus nasutus also shows some characteristics that are consistent with winter dormancy of adult females and copepodid stage V, although the results are equivocal. The day and night residence of most of the population in waters below 200 m, high wax ester content of females, and lack of evidence of deep in situ feeding in December are consistent with a dormancy response. However, a small mode of CVs and a few females were found in surface waters in December. Also, the metabolic potential of female *R. nasutus* collected at depth in December differed little from that of females collected near-surface in June. The stage structure was unusual in that females outnumbered CVs by 8:1 in winter. The metabolic enzyme/lipid index of dormancy (Fig. 12) that was useful for the other three species was not for *R. nasutus*, because June females had extremely high wax ester content and December females showed little reduction in metabolic enzymes. *R. nasutus* was also unusual in the large fraction of female body mass in the form of wax esters, a pattern not seen for any of the other species. If *R. nasutus* enters dormancy as females, they may have a similar capability for relatively rapid emergence as seen with *E. californicus*. Egg production experiments conducted with *R. nasutus* in the Southern California Bight and waters offshore showed consistently lower per capita fecundity than *C. pacificus* and a lack of correlation with ambient chlorophyll (Mullin, 1993). Mullin concluded that "... *Rhincalanus*" reproduction is more divorced from the immediate supply of food than is that of *Calanus*". This inference is consistent with the present finding of high wax esters in females, which may serve to buffer them from the effects of spatial variability in food supply.

Calanus pacificus californicus was particularly interesting because of the biphasic life history shown in this region. One segment of the population is active in surface waters

in December while another segment is dormant in subsurface waters. The surface-dwelling adult female *C.p. californicus* are active individuals, as shown by in situ grazing, release of eggs in both ambient and diatom-enriched seawater, and the activity of both metabolic enzymes. Yet, it was equally apparent that the deep winter layer of *C.p. californicus* CV was dormant, as shown by depressed activity of metabolic enzymes, lack of detectable chlorophyll pigments in gut contents, very high wax ester content, and continuous day-night residence in subsurface waters.

There appears to have been a small amount of exchange between the two segments of the *C.p. californicus* population. Although adult females were predominantly at the surface in winter, a smaller mode of females was in a subsurface layer overlapping the layer of CVs. These females had lower metabolic enzyme activity and higher wax ester content than surface females. Both of these properties were similar to the characteristics of the deep CVs when expressed on a mass-specific basis. These data suggest that a very small fraction of the deep dwelling CVs does molt to the adult stage at depth. We found adult male *C.p. californicus* and spermatophore-bearing females in this deep layer, both of which are consistent with this interpretation. Hence, a small fraction of the dormant layer of CVs must continue their development, after which the newly appearing adult females ascend into surface waters to feed and reproduce in winter.

These results reconcile and explain the apparent contradiction noted in the Introduction. Previous studies showing deep, quiescent layers of *C. pacificus* CV in the Southern California Bight (Alldredge et al., 1984; Osgood and Checkley, 1997) which are sometimes upwelled to the surface off Pt. Conception [Smith et al., 1986] and off Baja California (Longhurst, 1976; Alldredge et al., 1984) describe only part of the population, albeit the numerically dominant fraction. Studies showing continuous year-round presence of *C. pacificus* nauplii and adult females (Mullin and Brooks, 1967) and year-round egg production by *C. pacificus* (Mullin, 1991, 1993) reflect sampling of the near-surface fraction of the population. Clearly, any efforts to model the population growth of this species, one of the dominant species throughout the extent of the California Current System, must take account of these different sub-population segments.

Although the present sampling was conducted in a mild El Niño year (Lynn et al., 1995) and the abundance and egg production rate of *C. pacificus* were somewhat lower in winter 1992 than in winter of non-El Niño years (Mullin, 1997), we have seen no evidence that the dormancy responses of *C. pacificus* or other species were anomalous in our study year. The influence of stronger El Niño events on copepod dormancy characteristics has yet to be assessed.

The biphasic life history of *C.p. californicus* in this region at 33°N differs from the canonical pattern observed much further north at 48°N (Osgood and Frost, 1994). It is not clear what governs the “decision rules” that cause most individuals to remain dormant while a few continue their development to the adult stage. In these subtropical latitudes, where variations in primary production (Hayward et al., 1996) and zooplankton standing stock (Roesler and Chelton, 1987) are less seasonally predictable than in higher latitudes, selection for strongly seasonally synchronized timing of life history events may be much reduced. Where predation risk or food supply is much

less seasonally predictable, synchronous seasonal dormancy of an entire population would not confer consistent advantages over members of a population that remain active in the upper water column. A bet-hedging approach (Stearns, 1992) that permits some members of a population to respond year-round to favorable conditions for population growth appears to be more advantageous than a single, closely synchronized life history pathway. It would be particularly interesting to determine the processes that regulate which individuals proceed in their development and which enter a state of dormancy.

Further studies of the life history of *C.p. californicus* at intermediate localities in its range are needed before the differences at two latitudinal extremes can be ascribed to a latitudinal gradient. We note, however, that Marcus (1984) found latitudinal variations in the proportion of the population of *Labidocera aestiva* that produces diapause eggs.

In North Atlantic Slope water (ca. 40°N), Miller et al. (1991) found essentially all CIV, CV, adult male, and adult female *Calanus finmarchicus* in deep strata from June through February. In Korsfjord (60°12'N) near Bergen, Hirche (1983) found two differentiated vertical subpopulations of CV and adult female *Calanus finmarchicus* in both August and December. The deeper group was more quiescent, had lower ETS activity, and lower activity of digestive enzymes than the shallower group. This is an interesting parallel to the population of *C.p. californicus* observed in the present study. Pederson et al. (1995) also reported the occurrence of a small component of CIV, CV, and adult female *C. finmarchicus* in the upper 100 m in winter near 72°N. However, their population contrasts with Hirche's and with the present results, because the surface dwelling winter animals appeared to be dormant. They found no evidence of feeding or of molting of CIV or CV (Pederson et al., 1995). The biphasic life history of *C.p. californicus* differs from that of *C. hyperboreus* (Conover, 1988) and *Neocalanus tonsus* (Ohman, 1987). In the latter two species, females release eggs at depth in late winter and subsequently near the surface in spring, and there is no evidence for winter reproduction near the surface.

Metridia pacifica consistently showed no evidence of dormancy in the San Diego Trough. The coherent diel vertical migration pattern of all *M. pacifica* females in December as well as in June, together with their sustained grazing activity, relatively high metabolic enzyme activity, and relatively low lipid stores, are all consistent with active population growth. In Dabob Bay, *M. pacifica* (reported as *M. lucens*) sustained some winter reproduction, though much of the population remained at depth as females (Osgood and Frost, 1994). Still further north in the subarctic Pacific, *M. pacifica* females are present year-round, but the proportion of reproductively ripe females drops to 0 in December–January (Batchelder, 1985).

4.2. Suitability of dormancy measures

The two enzyme assays gave qualitatively similar results concerning the state of dormancy of a given species. However, the CS activity of *C.p. californicus* was consistently lower than the other three species, on either a protein-specific or animal-specific basis, regardless of developmental stage, depth, or time of year of sampling.

The explanation for this difference is not clear and will await experimental analysis of the relationship between CS activity and oxygen consumption rate. If there were a similar stoichiometry between CS activity and O_2 consumption for all four species, this would imply markedly greater metabolic efficiency in *C.p. californicus* than the other three species. Given the widespread occurrence of this species and the importance of its congeners in other oceanic realms, the metabolic efficiency of *Calanus* relative to other species warrants attention.

Berges et al. (1993) cautioned against comparing enzyme activities for animals of markedly different body sizes because of the mass dependence of respiration rate. However, the range of body size (as protein) here was only 4-fold among copepod species and < 2-fold within a species, suggesting that body size effects appear not to have confounded our results. Moreover, *Calanus* had lower (not higher) protein-specific CS activity than two larger-bodied species, contrary to predictions from allometric scaling. Body mass explained < 10% of the variability in protein-specific CS and ETS activity in the present data set. In this study, enzyme activities were influenced much more by the active or dormant state of the animals and by differences among species than by variations in copepod body mass.

Few previous analyses of CS activity of planktonic copepods have been reported. Clarke and Walsh (1993) measured activities equivalent to 15–35 pmol CS activity ($\mu\text{g protein}^{-1}$) for *Acartia tonsa* and *Temora longicornis*, if we assume that the protein content of those copepods was approximately half their dry mass. In other small planktonic crustaceans, *Artemia franciscana* of approximately 0.7–150 $\mu\text{g protein}$ content had CS activity of ca. 67–114 pmole CS activity ($\mu\text{g protein}^{-1}$) (Berges et al., 1993). These compare with 5–130 pmole CS activity ($\mu\text{g protein}^{-1}$) measured here.

Clarke and Walsh (1993) reported that the CS activity of two copepod species was depressed by starvation. Clarke et al. (1992) also reported generally higher CS activity of fish larvae (*Sciaenops ocellatus*) fed at higher food concentrations, especially in earlier age classes. The activity of glycolytic enzymes in adult fish is known to be sensitive to starvation (Lowery and Somero, 1990). Båmstedt (1980) reported that both ETS activity and respiration rate were lower in starved *Acartia tonsa*, while Berges et al. (1993) found no effect of food concentration on the CS activity of *Artemia franciscana*. In principle, the lowered enzyme activities measured in winter *C.p. californicus* CV and *E. californicus* in the present study could be influenced by lack of feeding rather than by quiescence per se. These two effects are rather difficult to distinguish in the field. However, the biomass and composition of microplankton (potential food) were not very different on these two cruises. Maximum concentrations of particulate C were 95–110 $\mu\text{g C L}^{-1}$ in both cases, while Chl *a* maxima were 2.0 and 1.2 $\mu\text{g Chl a L}^{-1}$ in June and December, respectively, with similar taxonomic compositions of phototrophic and heterotrophic microplankton from epifluorescence microscopy (F.M.H. Reid and M.D. Ohman, unpubl.). In addition, taken together with information on stage structure, diel vertical migration, egg production responses, and lipid studies, a dormancy-related reduction in enzyme activity is the most plausible explanation for the reduction observed here.

In this study, CS activity was uncorrelated with body size and appeared to be more sensitive than ETS activity to the physiological changes associated with dormancy. Also, CS is a single enzyme, while the ETS assay measures a complex of dehydrogenases. CS may thus prove to be a preferred index of metabolic potential in future zooplankton studies, especially when the relationship between respiration rate and enzyme activity is calibrated experimentally.

While the accumulation of storage lipids is a conspicuous accompaniment to dormancy for many species of marine copepods (e.g. Sargent and Henderson, 1986; Ohman et al., 1989; Hagen and Schnack-Schiel, 1996; Hirche, 1996), the interpretation of lipid content at any point in time can be ambiguous. The mass of storage lipids (principally wax esters and triacylglycerols) at any time reflects the equilibrium between biosynthesis and catabolism. Future uses of lipid assays for such issues would benefit from measures of lipid turnover rates rather than static measures of lipid mass alone.

The measures used here, taken together, gave rather clear interpretations of the state of dormancy/activity of the copepods, with the exception of *R. nasutus*. However, these are all indirect measures that, if taken in isolation, can be affected by other processes. It would be optimal to develop new measures that specifically assay the developmental arrest associated with dormancy. Proper calibration of CS activity may make this a very useful measure, as may new enzymatic measures of lipid turnover rates, enzymes associated with the molt cycle (Espie and Roff, 1995), assessment of the state of copepod tooth development (Miller and Nielsen, 1988), or perhaps assays for copepod molting hormones. Any such assay should be sufficiently sensitive to permit the analysis of individuals, so that the frequency of different dormancy states within a population can be assessed and the characteristics of individuals that complete their development can be distinguished from those individuals that arrest a developmental sequence by entering dormancy.

5. Conclusions

Copepod dormancy responses in the southern sector of the California Current System differ appreciably with the species of copepod considered. *Calanus pacificus californicus* shows continuous, year-round reproduction, with one segment of the population maturing and reproducing while another segment overwinters as copepodid stage V's. The decision rules that govern which individuals adopt these alternate pathways are not yet known. For *E. californicus*, CVs and adults both appear to be dormant in winter, yet females retain the capability to emerge relatively rapidly (< 3 d) when conditions are favorable. From these results, together with the capability for rapid reproduction when *E. californicus* are introduced into relatively food-rich coastal filaments (Smith and Lane, 1991), we hypothesize that *E. californicus* is an "event-driven" species with the capability to respond on a short-term basis to favorable environmental circumstances, and that this event time scale may be more important than seasonal phenomena in its life history. *R. nasutus* also should be

capable of initiating egg production relatively rapidly, since they will not need to molt first from copepodid stage V prior to egg production. However, the timing and stimuli for emergence from dormancy for this species are not yet clear. *M. pacifica* may be considered a continuous year-round occurring species in this region, with no evidence for seasonally interrupted population growth.

Calanus pacificus californicus and perhaps *Metridia pacifica* show less evidence of dormancy in this locality than further north in their geographic ranges. If the adaptive significance of dormancy for oceanic copepods rests upon seasonally predictable risks and benefits, then diminished seasonal predictability should alter the dormancy response. We suggest that reduced temporal autocorrelation of such factors as predation risk and food supply in these subtropical latitudes likely accounts for reduced coherence of copepod dormancy responses.

Models of pelagic ecosystems are sensitive to the initial conditions for seasonal population growth of zooplankton. As Carlotti and Radach (1996) noted, "... it is obvious that initial conditions influence the dynamics of both phytoplankton and *Calanus* populations". The present results show that such models need to be constructed with careful reference to the zooplankton species of interest and to geographic variations in life history characteristics.

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