



Grazing impact of mesozooplankton in an upwelling region off northern California, 2000–2003

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Abstract

Mesozooplankton ($>200\ \mu\text{m}$) grazing impact (% phytoplankton standing crop consumed d^{-1}) was determined by the gut fluorescence method during three springs (2000, 2001 and 2002) and two winters (2002 and 2003) in a coastal upwelling region off northern California. Wind events, in terms of both magnitude and duration, varied inter-annually and seasonally and included both upwelling-favorable and relaxation events. Grazing impact of mesozooplankton also varied inter-annually and seasonally, and was highest during June 2000 (mean = 129% of standing crop d^{-1}), a prolonged period of wind “relaxation” and phytoplankton bloom. In contrast, mean grazing impact was lower during periods of stronger, more persistent winds, more active upwelling, greater cross-shelf transport, and lower chlorophyll concentration (25% and 38% in May–June 2001 and 2002, respectively). Wintertime conditions (January 2002 and 2003) were characterized by weakly upwelling or downwelling-favorable winds, low chlorophyll concentration, and lower mean mesozooplankton grazing impact (13% and 12%, respectively). The larger ($>500\ \mu\text{m}$) size class contributed proportionally more to total mesozooplankton ($>200\ \mu\text{m}$) grazing impact than the smaller (200–500 μm) size class during all sampling periods except spring 2002. These results suggest that mesozooplankton grazing impact is higher in spring than in winter, and that during the spring upwelling season, grazing is higher during periods of wind relaxation (weak upwelling) than during periods of stronger upwelling. Further, these results suggest an important role of mesozooplankton grazers on phytoplankton dynamics in the upwelling region off northern California.

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1. Introduction

Coastal upwelling zones, particularly those associated with mid-latitude eastern boundary currents,

are known to be highly productive at lower trophic levels. Local wind forcing can directly affect (either positively or negatively) upwelling in these areas, depending on the wind intensity and direction. Furthermore, offshore transport of phytoplankton and zooplankton may increase as upwelling intensity and duration increase (Peterson, 1998; Botsford et al., 2003).

While numerous studies have addressed the zooplankton response to upwelling-induced phytoplankton

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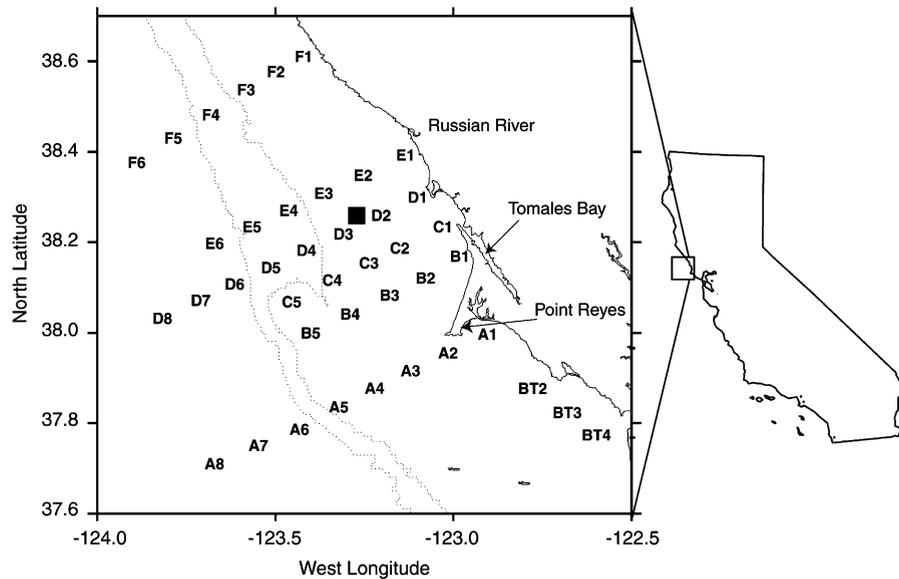


Fig. 1. Study region of CoOP-WEST. Station labels denote transect line (letter) and cross-shelf position (number). The central mooring (■) was located near station D2. Isobaths (200 and 1000 m) are represented by dotted lines (···).

increases (e.g., Boyd et al., 1980; Dagg et al., 1980; Fernandez, 1981; Cox et al., 1982; Peterson et al., 1988), the degree to which primary production and zooplankton grazing are coupled is still not clear. Mesozooplankton in coastal areas have been shown to directly utilize and effectively harvest a substantial part of the primary production (as much as 15–50% in non-tropical shelf areas) (Walsh, 1983; Baars and Fransz, 1984; Landry and Lorenzen, 1989; Bathmann et al., 1990). For example, Arinardi et al. (1990) reported that daily chlorophyll consumption by copepods was ca. four times higher during the chlorophyll-rich upwelling season than during the relatively chlorophyll-poor non-upwelling season in the Banda Sea. Peterson et al. (1988), however, showed that copepod gut fullness is not always correlated with changes in chlorophyll concentration during upwelling off Chile.

Wind-induced upwelling off northern California causes variation in phytoplankton production and standing crop that may, in turn, lead to variation in zooplankton grazing. This upwelling region includes a narrow shelf that experiences strong, equatorward winds in the spring and reversing winds in the winter, as well as wind relaxation events that result in a shift to northward and onshore water transport (Send et al., 1987; Wing et al., 1998). In spring, southward, upwelling-favorable wind events generally last 5–10 d and are separated by generally

shorter duration relaxation events (E. Dever, pers. comm.). Winter storms produce strong northward winds that last for several days and are followed by a rapid reversal to strong southward winds that taper until the onset of the next storm. This region (Fig. 1) was chosen for our study because it experiences strong upwelling-favorable winds and a wide variety of event durations (days to weeks), ensuring that the full range of responses to different wind forcing would be observed. Multiple cruises were conducted in spring (three cruises) and winter (two cruises) between 2000 and 2003 to assess biological and chemical responses to a variety of upwelling conditions.

Our objective was to determine the grazing impact of zooplankton on phytoplankton standing crop in the northern California upwelling region, as part of the interdisciplinary Coastal Ocean Processes—Wind Events and Shelf Transport (CoOP-WEST) program. To that end, we measured mesozooplankton gut pigment content (a proxy of gut content) as a means to assess recent ingestion of and relative grazing impact on phytoplankton. Despite some problematic issues inherent in the interpretation of data derived from this technique (e.g., varied feeding histories and lack of experimental acclimation of test organisms (Penry and Frost, 1991; Mayzaud and Razouls, 1992) and variation in pigment loss (Conover et al., 1986; Lopez et al., 1988)), it remains an efficient and

commonly used technique for the determination of in situ grazing rates on phytoplankton (Mackas and Bohrer, 1976; Boyd et al., 1980; Nicolajsen et al., 1983; Peterson et al., 1990a; Saiz and Alcaraz, 1990; Echevarria et al., 1994; Bode et al., 2003). We, therefore, chose to use the gut fluorescence technique as a tool with which to measure the relative grazing impact of mesozooplankton grazers on phytoplankton standing crop in an upwelling region off northern California. Both inter-annual and seasonal variability are discussed.

2. Materials and methods

Mesozooplankton samples were collected, size fractionated and analyzed for gut pigment content during three spring and two winter cruises between 2000 and 2003 (Table 1).

2.1. Wind data collection

Hourly values of wind speed and direction were downloaded from the NDBC website for station 46013 (Bodega Bay station at 38°13'37"N, 123°19'48"W) for springs 2000, 2001, 2002 and winter 2003. Since station 46013 did not report data during January 2002, wind data were collected from NDBC Station 46026 (37°45'32"N 122°50'00"W), located approximately 75 km to the southeast (see Dorman et al., 2005, for details on correlation analyses run between these two NDBC stations and the justification for using NDBC Station 46026 in winter 2002). Wind direction was rotated 35° according to the orientation of the central California coastline, and adjusted wind direction data were used to calculate alongshore and cross-shelf components of wind speed data. Expected hourly cross-shelf Ekman transport values based on the along-shore wind vector and Coriolis were calculated

according to Bakun (1973) and a 15-h moving average was applied.

2.2. Mesozooplankton collection

Vertically integrated mesozooplankton samples were collected with a 1-m (spring 2000) or 0.5-m (2001–2003) diameter, 73- μm mesh ring net towed vertically at a wire speed of 10 m min^{-1} from a depth of 200 m (or 5 m off the bottom, whichever was shallower) to the surface. The exact depth stratum sampled was determined after each tow using a Vemco Minilog-TDR depth recorder (2001–2003). Water volume filtered during the net tow was determined by a digital flowmeter (General Oceanics Inc.) attached across the mouth of the net. The flowmeter rotor was held by the net as it billowed up through the mouth of the ring slightly, preventing it from spinning, during each downcast. Nets were rinsed and cod end contents immediately narcotized with 10% carbonated water (final concentration, v/v) to minimize stress and gut evacuation of zooplankton (Gannon and Gannon, 1975; Kleppel and Pieper, 1984). A subsample (typically ~1–10% of sample) was then removed using a 10-mL Stempel pipette and processed for gut pigment content. Timing of gut pigment sampling occurred throughout the day and night, and was therefore independent of any diel feeding cycles that have been observed in some grazers (e.g., copepods; Mackas and Bohrer, 1976; Dagg et al., 1989; Peterson et al., 1990b). The remainder of the sample was preserved in 7–10% (final concentration) borate-buffered formalin for later microscopic analyses. Zooplankton were subsequently identified and enumerated (see Dorman et al., 2005 and Papastephanou et al., 2006, for euphausiids and copepods, respectively).

Zooplankton biovolume measurements were obtained from samples collected by bongo net tows at stations A1–4, A6, A8, D1–4, D6, D8, F1–4 and F6. Paired bongo nets (0.6 m diameter, fitted with 335- μm and 500- μm mesh) were towed obliquely at a ship speed of 2 knots and hauled back at 10 m min^{-1} . The exact depth stratum sampled for each net tow was determined after each tow using a Vemco Minilog-TDR depth recorder. The volume of water filtered during each net tow was determined by a digital flowmeter (General Oceanics Inc.) attached across the mouth of each net. Samples were preserved in 7–10% (final concentration) borate-buffered formalin or 70% (final concentration)

Table 1
Summary of sampling of mesozooplankton gut pigment

Cruise season, year	Dates sampled (<i>n</i>)	Total <i>n</i> per cruise
Spring 2000	June 24(4), 27(2), 28(2), 29(3)	11
Spring 2001	June 3(3), 5(5), 6(2), 13(1)	11
Spring 2002	June 18(3), 24(4), 25(5), 26(4)	16
Winter 2002	January 12(5), 18(3)	8
Winter 2003	January 11(5), 20(5)	10

n = number of samples.

ethanol. Total biovolume for each sample (all individuals <5 mL displacement volume) was determined by the displacement volume method (Tranter, 1959). While these samples were collected using a different net system than those used for gut fluorescence estimates, the 335- and 500- μm mesh sizes are comparable to grazing estimate size fractions (e.g., 200–500, >500 μm) and are therefore meaningful when making interannual and seasonal comparisons of zooplankton biovolumes during our study.

2.3. Gut pigment analysis

Mesozooplankton grazing impact was estimated using the gut fluorescence method (Mackas and Bohrer, 1976). Mesozooplankton were wet-sieved over nested sieves of 500-, 200- and 73- μm Nitex mesh immersed in 5- μm -filtered seawater to produce three size fractions of grazers: >500, 200–500 and 73–200 μm .

We chose to measure grazing of three size classes rather than individual species of mesozooplankton for several reasons. First, processing and analyzing samples for multiple species was beyond the scope of the overall project and our limited personnel and ship-board bunk space. Second, zooplankton rate processes are generally size-dependent (Huntley and Boyd, 1984; Peters and Downing, 1984; Ikeda, 1985) and rates based on size classes have proven useful in modeling plankton communities (Platt, 1985; Dickie et al., 1987; although see Frost, 1980). Finally, zooplankton size classes have been used successfully in grazing estimates (Morales et al., 1990, 1991; Bautista and Harris, 1992; Morales et al., 1993).

Subsamples processed for gut pigment content were filtered onto 47-mm diameter GF/F filters, wrapped in foil, flash frozen and stored in liquid nitrogen until pigment extraction. Three equal, random subsamples were obtained from each frozen filter using a handheld hole punch, homogenized in 90% acetone using a motorized tissue homogenizer, and filtered across 25-mm GF/F filters to remove pulp. The filtrate containing extracted gut pigment was measured before and after acidification with 10% hydrochloric acid on a Turner 111 (2000) or Turner 10 (2001–2003) fluorometer according to Strickland and Parsons (1972). All three mesozooplankton size fractions were processed and analyzed, but, on some occasions, significant phytoplankton blooms (containing predominantly the large chain-forming diatom *Chaetoceros* sp.)

clogged the net and 73- μm mesh sieve such that diatoms were likely carried over to GF/F filters during subsampling of the smallest size fraction. To minimize misinterpretation of gut pigment content related to this form of contamination, we report data from only the two larger size fractions: 200–500 and >500 μm .

Gut pigment content (GP, $\mu\text{g pigment L}^{-1}$) was calculated using the following equation:

$$\text{GP} = \frac{\text{GP}_{\text{sub}} \times \text{A}_{\text{tot}}}{\text{A}_{\text{sub}} \times \text{P} \times \text{V}}, \quad (1)$$

where GP_{sub} is the concentration of gut pigment ($\mu\text{g phaeopigment L}^{-1}$) from the subsample, A_{tot} and A_{sub} the total and subsampled areas (mm^2) of the filter, P the proportion of sample processed for gut pigment content and V the volume of water filtered (L) during each net tow. We report gut pigment values as phaeopigment rather than chlorophyll since chlorophyll *a* is not universally accepted as a conservative tracer of feeding processes (Conover et al., 1986; Penry and Frost, 1990).

2.4. Calculation of grazing impact

Grazing impact of mesozooplankton (GI, % of phytoplankton standing crop grazed d^{-1}) was calculated using the following equation:

$$\text{GI} = \frac{\text{GP} \times \text{CR}}{\text{SC}} \times 100, \quad (2)$$

where GP ($\mu\text{g phaeopigment L}^{-1}$) is the concentration of gut pigment, CR the gut clearance rate (2.0 h^{-1} , from Dagg et al., 1989, $\times 24 \text{ h d}^{-1}$) and SC the phytoplankton (chlorophyll) standing crop ($\mu\text{g chlorophyll } a \text{ L}^{-1}$).

No correction was made for possible pigment destruction. Reports of pigment loss to non-fluorescent compounds during copepod digestion vary widely (0–95% loss of ingested chlorophyll) with varying phytoplankton pigment composition, ingestion rate, gut residence time, enzyme activity and acclimation (i.e., feeding history) (Conover et al., 1986; Lopez et al., 1988; Penry and Frost, 1990, 1991; Head and Harris, 1992; Mayzaud and Razouls, 1992; Tirelli and Mayzaud, 1998).

Gut clearance rate (a proxy for ingestion rate) determination requires a high number of samples (see Irigoien, 1998, for review) and was beyond the scope of our study. We therefore chose to use a published gut evacuation rate of 2.0 h^{-1} (determined by Dagg et al., 1989). It is important to note that

these rates are temperature dependent (Dam and Peterson, 1988) and could be higher or lower than the constant value we used in our calculations.

2.5. Phytoplankton (chlorophyll) standing crop

Chlorophyll data were kindly provided by R. Dugdale and F. Wilkerson; full details on sample collection and processing can be found in Wilkerson et al. (2006) but are briefly described here. Two hundred and eighty milliliter (or 50 mL during significant “blooms”) of water collected from 5 m by 12-L Niskin bottles were filtered onto 47-mm diameter GF/F filters (0.7 μm nominal pore size) and stored in a 4 °C freezer until extraction and analysis in the lab (typically < 2 weeks). Chlorophyll was extracted in 90% acetone at room temperature in the dark for 24 h and read (before and after acidification with three drops of 10% hydrochloric acid) on a Turner 10 (2000–2002) or Turner 10AU (2003) fluorometer according to Strickland and Parsons (1972). All fluorometers were previously cross-calibrated to ensure consistent readings between machines.

Estimates of instantaneous phytoplankton growth were determined during all cruises (data kindly provided by R. Kudela, data unpublished), using measured primary productivity rates ($\text{mg C m}^{-2} \text{d}^{-1}$), chlorophyll values ($\mu\text{g chlorophyll L}^{-1}$) and an average C:Chl ratio of 100:1.

2.6. Statistical analyses

Data were analyzed using nonparametric statistics, following Levene’s Test for Homogeneity of Variances, with one exception (onshore–offshore comparison of grazing impact by the > 500- μm size class) where a one-way analysis of variance (ANOVA) was used. A significant result ($p < 0.05$) from a Kruskal–Wallis ANOVA was then followed by Mann–Whitney U (MWU) tests to distinguish statistically significant differences between means. Type I error values ($\alpha = 0.05$) were adjusted using the Bonferroni technique when multiple comparisons were performed (Sokal and Rohlf, 1995).

3. Results

3.1. Wind, upwelling and phytoplankton (chlorophyll) standing crop

Wind conditions, upwelling indices and chlorophyll concentrations during the sampling cruises varied

seasonally and inter-annually. Each of the three spring and two winter cruises is described in turn below.

June 2000 was characterized by a prolonged “relaxation” period (Fig. 2A), with generally low winds in early June, modest upwelling-favorable wind events mid-month, and generally weak equatorward winds in late June. Such conditions set up a phytoplankton bloom comprised predominantly of the large ($\sim 15\text{-}\mu\text{m}$, non-chain-forming, A. Lassiter and F. Wilkerson, pers. comm.) diatom *Chaetoceros* sp., with peak concentrations in early June ($32 \mu\text{g chlorophyll } a \text{ L}^{-1}$) at station D2 as well as off Point Reyes and over the shelf (station D1) (Fig. 3A). Nanoflagellates ($\sim 2.5\text{--}5 \mu\text{m}$) dominated the phytoplankton assemblage in late June (June 29) (A. Lassiter, unpublished data; see also Table 2).

Spring (May 17–June 15) 2001, in contrast, was characterized by stronger, more persistent upwelling-favorable winds (Fig. 2B). A brief phytoplankton bloom (peak = $14 \mu\text{g chlorophyll } a \text{ L}^{-1}$) dominated by *Chaetoceros* sp. was observed during a relaxation event June 3–4, but overall, chlorophyll concentrations were considerably lower (mean = $0.9 \mu\text{g chlorophyll } a \text{ L}^{-1}$) than in June 2000 (mean = $2.7 \mu\text{g chlorophyll } a \text{ L}^{-1}$) (Table 2, Fig. 3B). Persistent winds during early June (June 6) led to deeper mixing and smaller phytoplankton cells (e.g., *Synechococcus* < 2 μm and nanoflagellates > 2.5 μm) than in spring 2000 (A. Lassiter, unpublished data).

Spring (May 30–June 28) 2002 sampling was preceded by brief upwelling and “relaxation” periods. Stronger, persistent upwelling-favorable winds were observed during sampling, resulting in somewhat higher overall upwelling in spring 2002 than in spring 2001 (Fig. 2C). Mean phytoplankton standing crop concentration was higher (mean = $2.9 \mu\text{g chlorophyll } a \text{ L}^{-1}$) than in spring 2001 ($0.9 \mu\text{g chlorophyll } a \text{ L}^{-1}$) (Table 2, Fig. 3C), consisting primarily of *Chaetoceros* sp. and *Thalassiosira* sp. (June 25) (A. Lassiter, unpublished data).

Winter (January 14–23) 2002 winds produced weak upwelling conditions (Fig. 2D) and had a stronger cross-shelf component (onshore flow in the surface layer, see Dorman et al., 2005) relative to spring. Four-fold increases in phytoplankton standing crop concentrations were observed at times but were not considered blooms, as concentrations remained relatively low (mean = $1.1 \mu\text{g chlorophyll } a \text{ L}^{-1}$) (Table 2, Fig. 3D). The phytoplankton assemblage was dominated by nanoflagellates ($\sim 2.5\text{--}5 \mu\text{m}$) and *Synechococcus* sp. (< 2 μm) and contained fewer diatoms than spring assemblages (A. Lassiter, unpublished data).

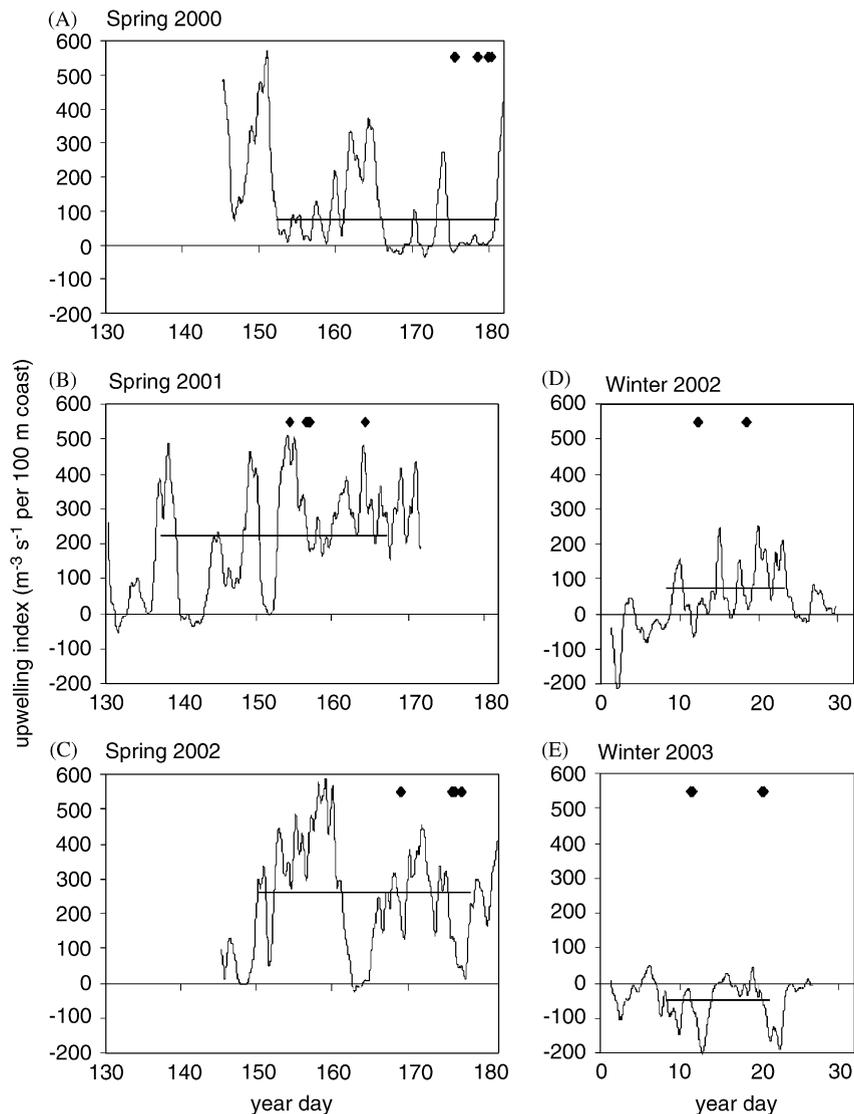


Fig. 2. Upwelling indices (15-h averaged hourly data —, cruise mean —) and grazing sampling dates (◆) for (A) spring 2000, (B) spring 2001, (C) spring 2002, (D) winter 2002, and (E) winter 2003. Mean upwelling index for each cruise was 77 (spring 2000), 223 (spring 2001), 259 (spring 2002), 73 (winter 2002) and -50 (winter 2003).

Winter (January 14–21) 2003 was characterized by downwelling favorable winds (Fig. 2E) and relatively low phytoplankton standing crop (mean = $1.7 \mu\text{g}$ chlorophyll $a L^{-1}$) (A. Lassiter, unpublished data). Phytoplankton assemblage data for this period are not available.

3.2. Gut pigment and grazing impact—spatial and temporal variability

Spatial variability in gut pigment and grazing impact was apparent for all sampling periods in

both size fractions (Figs. 4–7) yet no consistent pattern was apparent. Therefore, we pooled grazing impact data from all cruises (binned by size class) to test for differences related to onshore (< 200 m bottom depth, $n = 41$) vs. offshore (> 200 m bottom depth, $n = 15$) stations. Grazing impact by 200–500- μm zooplankton was higher at onshore stations (20% phytoplankton consumed d^{-1}) than offshore stations (6% phytoplankton consumed d^{-1}) ($p = 0.018$, Kruskal–Wallis test) (Table 3, Fig. 6). In contrast, onshore–offshore differences in grazing impact by the > 500 - μm size class were suggestive of

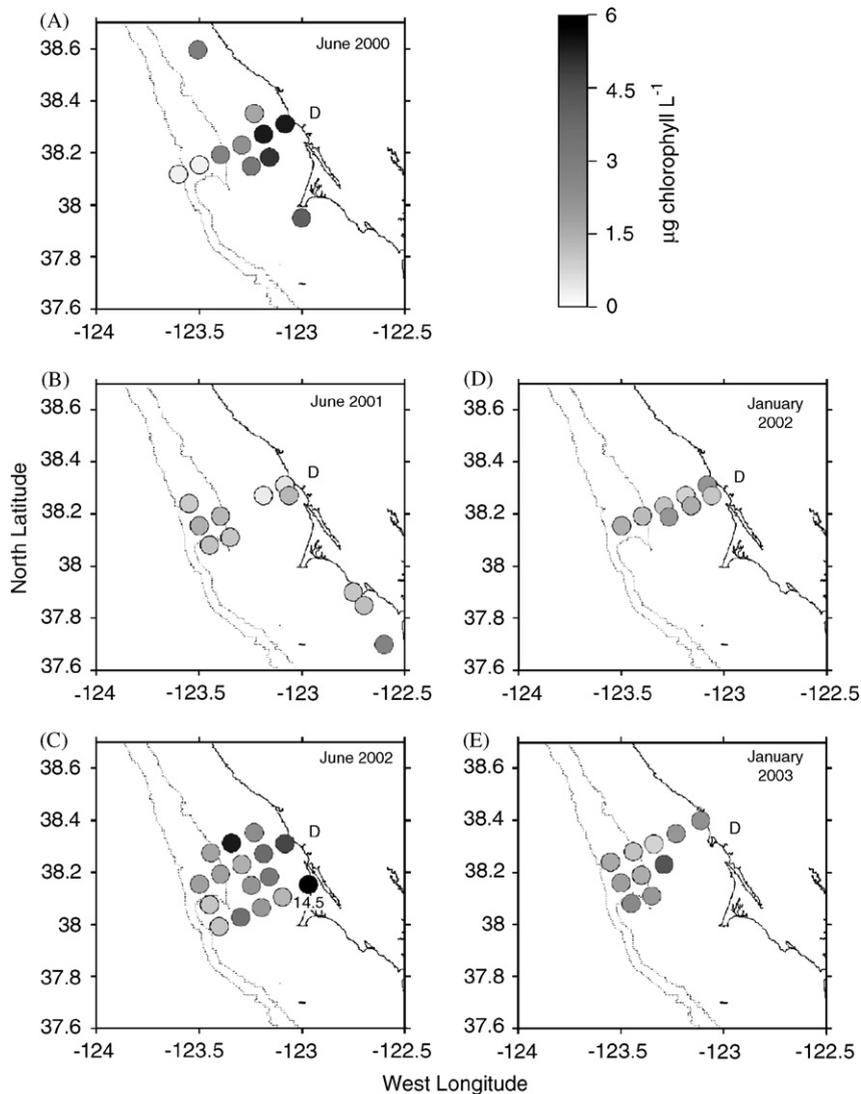


Fig. 3. Phytoplankton (chlorophyll *a*) standing crop concentrations during (A) spring 2000, (B) spring 2001, (C) spring 2002, (D) winter 2002 and (E) winter 2003. Overlapping data bubbles indicate the collection of more than one sample.

an opposite trend (24% vs. 40%, respectively) but were not statistically significantly different ($p = 0.316$, one-way ANOVA) (Table 3, Fig. 7).

With respect to temporal differences, mean grazing impact of mesozooplankton $> 200 \mu\text{m}$ varied inter-annually, particularly during spring (i.e., upwelling season) (Fig. 8). Spring 2000 mean grazing impact was significantly higher than spring 2001 ($p < 0.001$, Mann–Whitney *U* test) and spring 2002 ($p = 0.003$, Mann–Whitney *U* test). Wintertime mean grazing impacts, on the other hand, were not significantly different from one another.

Seasonal variation of mesozooplankton grazing impact on phytoplankton also was observed

(Figs. 6–8). Mean grazing impact of mesozooplankton $> 200 \mu\text{m}$ was significantly higher in spring (61%) than in winter (13%) ($p < 0.001$, Mann–Whitney *U* test) (Table 5, Fig. 8). Both 200–500- and $> 500\text{-}\mu\text{m}$ size classes were also significantly higher in spring than winter ($p < 0.001$ and $p = 0.003$, respectively, Mann–Whitney *U* test).

Springtime mesozooplankton community composition was relatively similar between years, dominated by copepod nauplii (typically $> 25\%$ of individuals), *Oithona similis*, *Pseudocalanus* spp., *Microsetella rosea* and *Acartia* spp., depending on station location (Table 5). Wintertime assemblages differed somewhat from springtime assemblages,

Table 2
Summary of phytoplankton (chlorophyll) standing crop concentrations

	Mean (SE) station D2 ($\mu\text{g chl L}^{-1}$)	Peak station D2 ($\mu\text{g chl L}^{-1}$)	Mean (SE) all stations sampled ($\mu\text{g chl L}^{-1}$)	Mean (SE) gut pigment stations only ($\mu\text{g chl L}^{-1}$)	Numerically dominant phytoplankton taxa present ^a
Spring 2000	10.3 (1.7)	32.1	5.7 (0.4)	2.7 (0.6)	Nanoflagellates, picoflagellates (June 29)
Spring 2001	4.6 (1.1)	14.5	2.6 (0.2)	0.9 (0.2)	<i>Synechococcus</i> sp., nanoflagellates (June 6)
Spring 2002	3.0 (1.0)	12.2	3.2 (0.4)	2.9 (0.8)	<i>Chaetoceros</i> sp., <i>Thalassiosira</i> sp. (June 25, station D1); <i>Chaetoceros</i> sp., centric diatom (June 25, station D3); <i>Chaetoceros</i> sp., nanoflagellates (June 24, station C2)
Winter 2002	0.8 (0.1)	1.6	1.2 (0.1)	1.1 (0.1)	Nanoflagellates, <i>Synechococcus</i> sp. (January 12); <i>Synechococcus</i> sp., picoflagellates, monads, Chroomonas, nanoflagellates (January 18)
Winter 2003	1.4 (0.2)	2.4	1.4 (0.1)	1.7 (0.3)	Not available

SE = standard error.

^aAt station D2, or closest station available (in **bold**), at time of mesozooplankton gut pigment sampling.

containing predominantly copepod nauplii, *O. similis*, *Oncea* spp. and *Clausocalanus* spp. While we did not size-fraction preserved samples during microscopic analyses, estimates of individual sizes would put small copepods (e.g., *Oncea* spp.) and copepod nauplii in the 200–500- μm size class and most other mesozooplankton in the >500- μm size class. Our samples included other common zooplankton taxa (e.g., *Calanus* spp., *Paracalanus* spp., *Ctenocalanus* sp., *Metridia lucens* (*pacifica*), *Euphausia pacifica*, *Thysanoessa spinifera*) but not in high enough abundances to fall within the four numerically dominant taxa listed in Table 5.

Zooplankton biovolumes showed inter-annual and seasonal variation as well (Table 4). Biovolumes of zooplankton (>335 and >500 μm) were higher in spring than in winter. It should be noted that these mean zooplankton biovolumes include stations sampled farther offshore than gut fluorescence samples and comparisons between trends seen in grazing impacts and zooplankton biovolume should be considered with caution.

3.3. Contribution of size classes to total grazing impact

Overall, grazing impact by the larger (>500 μm) mesozooplankton size class exceeded that of the

smaller (200–500 μm) size class (Table 3, Figs. 6–8). For instance, the larger size class contributed 68% (springs 2000 and 2001) to 82% (winter 2003) of the total (>200 μm) mean grazing impact. The only exception to this pattern was spring 2002, when grazing by the 200–500- μm size fraction contributed 55% to total mean grazing impact (Table 3, Figs. 6–8).

Estimates of instantaneous phytoplankton growth were determined during all cruises (R. Kudela, data unpublished), but few were taken concurrently with gut pigment estimates. Nonetheless, some were appropriate (i.e., overlapped temporally and spatially) with gut pigment sampling to allow comparison of mesozooplankton grazing impact (% phytoplankton removal d^{-1}) to phytoplankton growth (% phytoplankton increase d^{-1} , calculated from instantaneous growth rate assuming exponential growth). A more conventional approach would have been to compare mesozooplankton ingestion rates with primary productivity rates (e.g., Dagg, 1993; Morales et al., 1993; Dam et al., 1995). While primary productivity ($\text{mg C m}^{-2} \text{d}^{-1}$) was measured on some of our cruises, no C:Chl ratios were derived empirically. Therefore we chose to compare our pigment-based mesozooplankton ingestion rates and grazing impact to phytoplankton growth as measured in % population increase per day (Fig. 8).

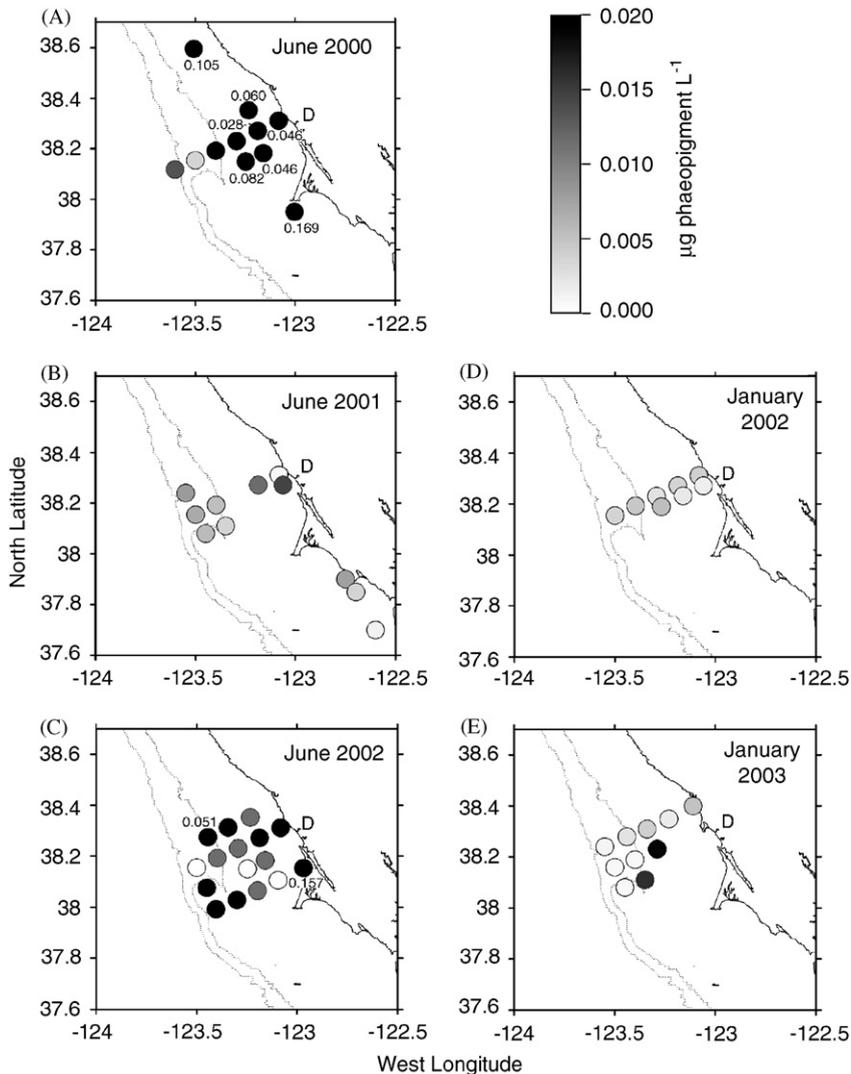


Fig. 4. Mesozooplankton (>200 μm) gut pigment concentration during (A) spring 2000, (B) spring 2001, (C) spring 2002, (D) winter 2002 and (E) winter 2003. Overlapping data bubbles indicate the collection of more than one sample.

In general, phytoplankton growth rates increased with increased upwelling intensity and were lower in winter than in spring.

4. Discussion

The average impact of mesozooplankton grazers on oceanic phytoplankton primary production at a global scale has been reported to be ca. 12% (Calbet, 2001). In terms of daily removal of phytoplankton standing crop, others have reported estimates rarely exceeding 30% in temperate latitudes (Huskin et al., 2001). At tropical latitudes, Rollwagen Bollens and Landry (2000) showed that mesozooplankton (202–2000 μm) responded to a

phytoplankton bloom with an increase in grazing impact, with higher values inside the bloom patch (14%) than outside (6%). In upwelling areas, grazing impact on available phytoplankton biomass has been reported to be generally low (<25%) (Landry and Lorenzen, 1989; Peterson et al., 1990b; Verheye et al., 1992; Painting et al., 1993). Overall, our estimates of mesozooplankton grazing impact on phytoplankton standing crop in the northern California upwelling system are consistent with this range of reported values, with the exception of our high values in spring 2000.

One of the primary differences between springs of 2000, 2001 and 2002 was the duration of wind stress and the subsequent differences in phytoplankton

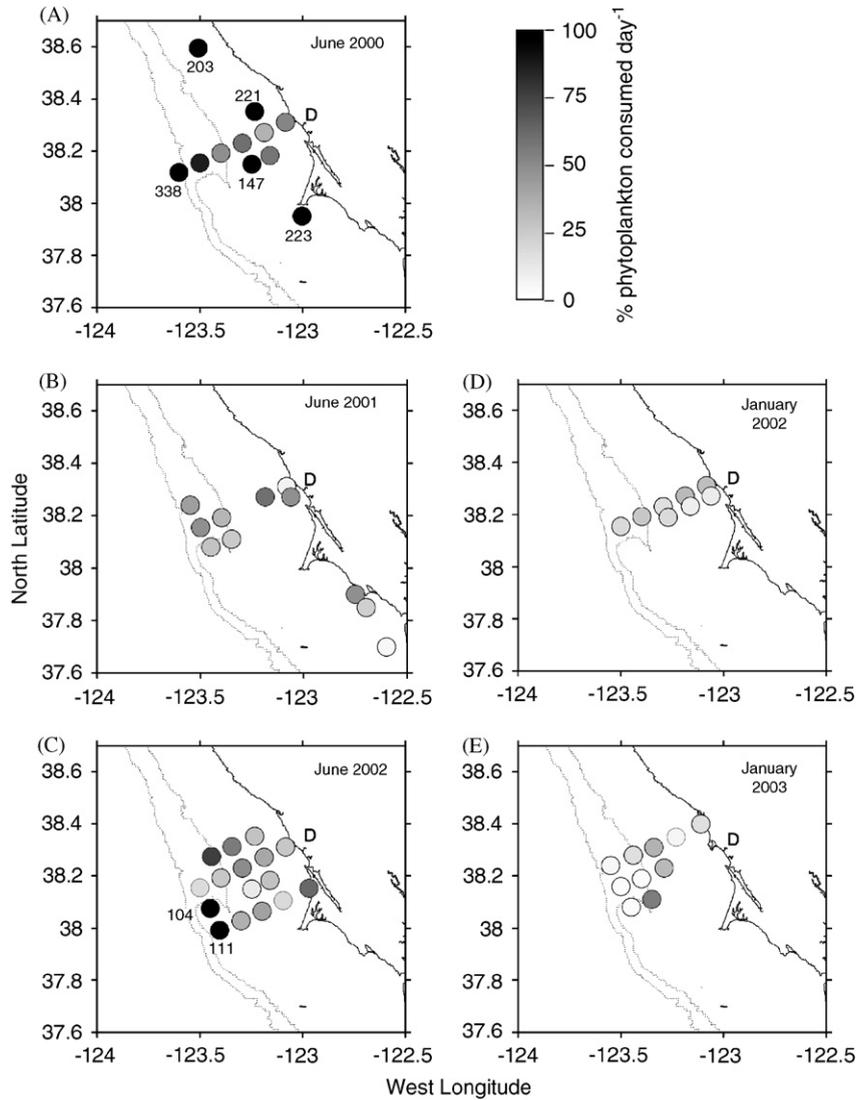


Fig. 5. Mesozooplankton ($>200\ \mu\text{m}$) grazing impact on phytoplankton standing crop during (A) spring 2000, (B) spring 2001, (C) spring 2002, (D) winter 2002 and (E) winter 2003. Overlapping data bubbles indicate the collection of more than one sample.

bloom development and community composition. Mesozooplankton community composition was similar during springs 2000, 2001 and 2002 (Table 5). However, Wilkerson et al. (2006) observed a switch in the phytoplankton community from 10 to $15\text{-}\mu\text{m}$ diatoms (e.g., *Chaetoceros* sp. and *Thalassiosira* sp.) to smaller cells (e.g., $2.5\text{--}5\text{-}\mu\text{m}$ nanoflagellates) between early and late June 2000. In addition, spring 2001 differed from springs 2000 and 2002 in that the phytoplankton assemblage was dominated by even smaller ($<2\ \mu\text{m}$) picoplankton cells (e.g., *Synechococcus* sp.), compared to $2.5\text{--}5\text{-}\mu\text{m}$ cells in late June 2000 and $10\text{--}15\text{-}\mu\text{m}$ cells in late June 2002.

Changes in the phytoplankton community assemblage from diatoms to smaller flagellated cells, as was observed in this study, may affect mesozooplankton grazing and gut pigment content. Several studies have found that food particle size is important in determining feeding behavior of suspension-feeding zooplankton (Rothhaupt, 1990a,b). In particular, Nival and Nival (1976) suggested *Acartia* copepods are unable to feed on particles $<3\ \mu\text{m}$, and Calbet et al. (2000) showed that *Oithona* females (in Kaneohe Bay, Hawaii) fed well on nanoplankton ($2\text{--}5\ \mu\text{m}$) but not on picoplankton ($<2\ \mu\text{m}$). These observations may help to explain lower grazing impacts when phytoplankton

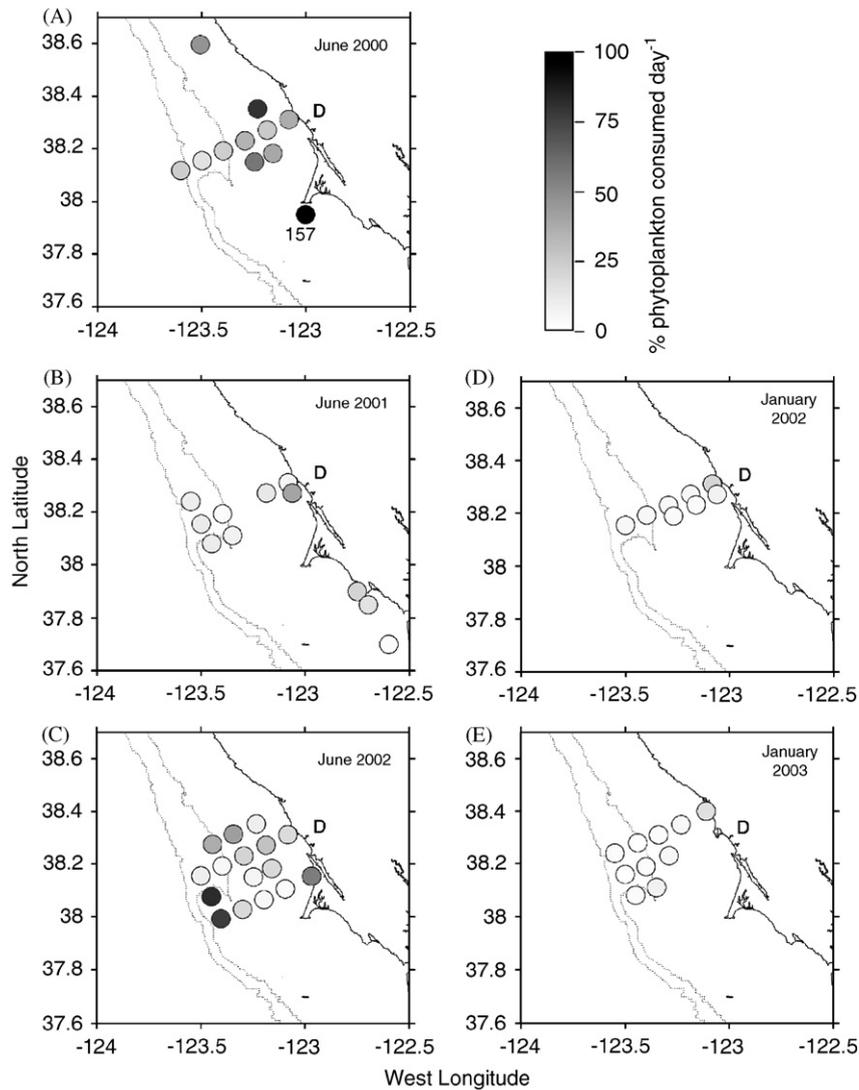


Fig. 6. Mesozooplankton (200–500 μm) grazing impact on phytoplankton standing crop during (A) spring 2000, (B) spring 2001, (C) spring 2002, (D) winter 2002 and (E) winter 2003. Overlapping data bubbles indicate the collection of more than one sample.

assemblages were dominated by picoplankton cells (e.g., *Synechococcus* sp. in spring 2001) vs. nanoplankton and diatoms (in spring 2000).

High grazing estimates during spring 2000 also occurred toward the end of a significant diatom (*Chaetoceros* sp.) bloom. These observations are consistent with Painting et al. (1993), who reported copepod feeding in the southern Benguela upwelling system to be higher toward the end of the bloom (38% grazing impact) than in maturing upwelled waters (5–10% grazing impact). Gowen et al. (1999) also reported higher grazing impact toward the end of the spring bloom in the western Irish Sea (56%

and 150% of daily phytoplankton production at onshore and offshore stations, respectively). They attributed this trend to increased zooplankton abundance, consistent with the classical phytoplankton–zooplankton bloom pattern in which there is a lag between maximum spring bloom standing crop and copepod abundance (Cushing, 1989). Indeed, an increase in nanoflagellates and dinoflagellates following the decline of a phytoplankton bloom has been shown to result in lower gut fluorescence values in copepods (> 300 μm) in other temperate regions (Nicolajsen et al., 1983). Moreover, cyanobacteria (e.g., *Synechococcus*) are

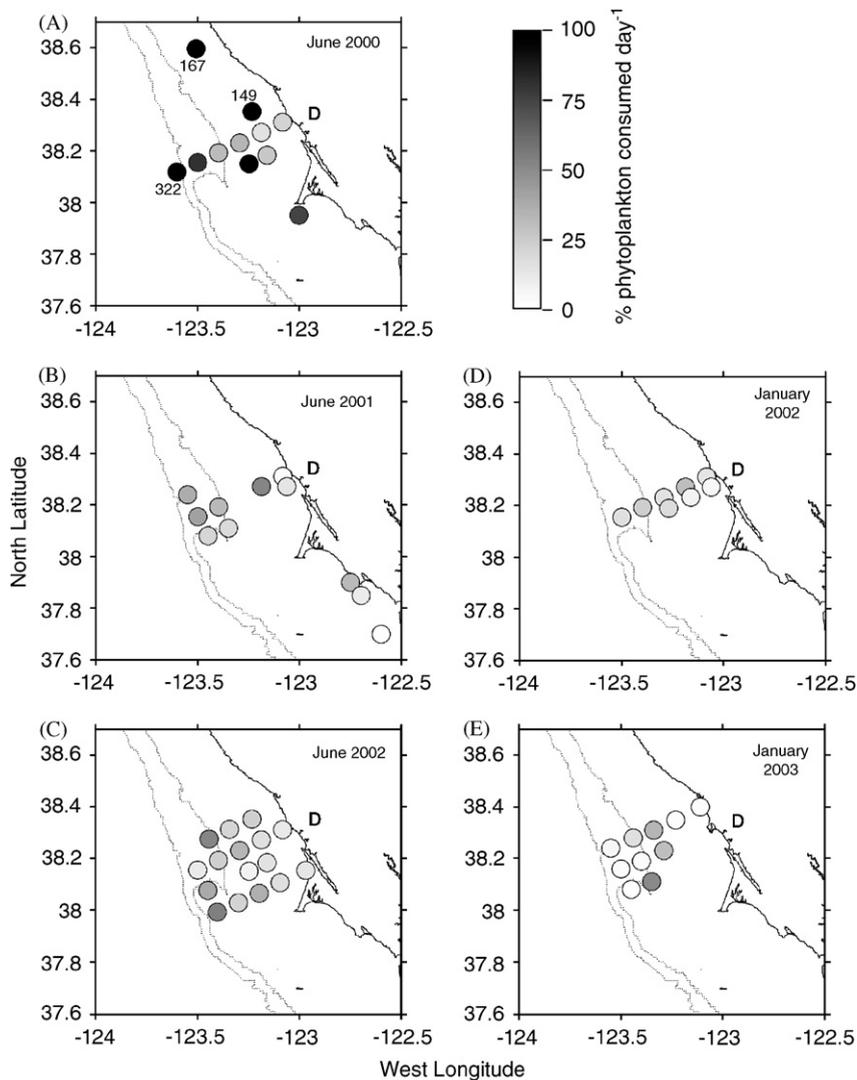


Fig. 7. Mesozooplankton ($>500\ \mu\text{m}$) grazing impact on phytoplankton standing crop during (A) spring 2000, (B) spring 2001, (C) spring 2002, (D) winter 2002 and (E) winter 2003. Overlapping data bubbles indicate the collection of more than one sample.

Table 3

Mean (SE) grazing impact of mesozooplankton (% phytoplankton consumed day^{-1}) by shelf position

	Offshore ($>200\ \text{m}$ water depth)	Onshore ($<200\ \text{m}$ water depth)
$>200\ \mu\text{m}$ (total)	46.2 (11.9)	44.8 (7.0)
200–500 μm	6.0 (1.6)	20.3 (3.2)
$>500\ \mu\text{m}$	40.2 (10.4)	24.5 (3.8)
<i>n</i>	15	41

n = number of samples.

frequently considered of low nutrient quality (Gliwicz and Lampert, 1990) and may be a less preferred food source.

With regard to seasonal variability, grazing impact was generally higher during the spring and lower during the winter (Fig. 8). This is consistent with Runge (1980) who reported seasonality in grazing activity in *Calanus pacificus* in a temperate fjord where maximum clearance rates were associated with the spring bloom. Similarly, Mackas and Burns (1986) found that *C. pacificus* had higher filtration rates in experiments run in spring and early summer than in winter. Our findings, along with other investigations, are consistent with the observation that wintertime conditions in temperate marine ecosystems can present physiological challenges to mesozooplankton (food resources are generally in low concentration, grazers may be

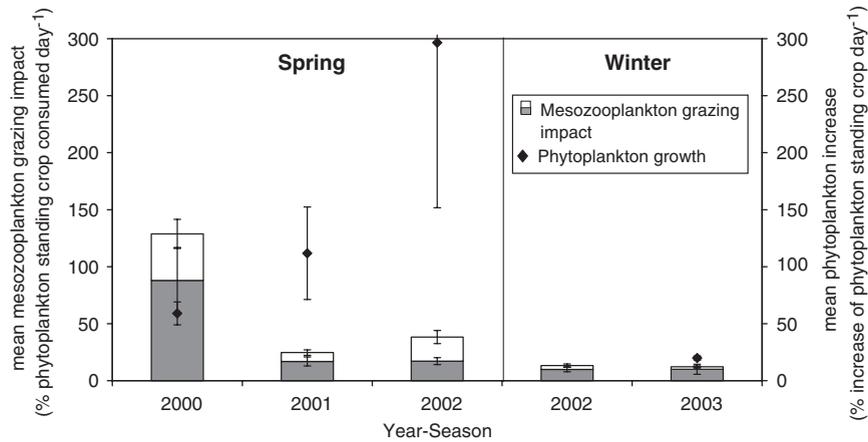


Fig. 8. Mean (\pm standard error) daily mesozooplankton grazing impact on phytoplankton standing crop (■ > 500 μm , □ 200–500 μm) and phytoplankton growth, spring 2000 through winter 2003. Sample sizes for mean phytoplankton growth estimates were $n = 5$ (spring 2000), $n = 4$ (spring 2001), $n = 2$ (spring 2002), $n = 0$ (winter 2002) and $n = 2$ (winter 2003).

Table 4
Zooplankton biovolume (mL m^{-3}) from 335 and 500 μm mesh bongo net tows

	Size class (μm)	Mean (SE)	n
Spring 2000	> 335	0.52 (0.06)	27
	> 500	0.40 (0.04)	28
Spring 2001	> 335	0.43 (0.05)	32
	> 500	0.33 (0.04)	33
Spring 2002	> 335	0.49 (0.04)	17
	> 500	NA	
All springs (2000–2002)	> 335	0.47 (0.03)	76
	> 500	0.36 (0.03)	61
Winter 2002	> 335	0.33 (0.03)	26
	> 500	0.26 (0.03)	26
Winter 2003	> 335	0.24 (0.03)	17
	> 500	0.18 (0.04)	17
All winters (2002–2003)	> 335	0.29 (0.03)	43
	> 500	0.23 (0.02)	43

SE = standard error; n = number of samples; NA = not available.

recovering from diapause or nutritional deprivation). Estimates of primary production taken at select grazing stations in this study (R. Kudela, unpublished data) suggest that phytoplankton grow faster during the spring than in winter, and during the upwelling season their growth rates are generally higher following moderate upwelling and relaxation events. Furthermore, many physiological processes (e.g., growth, reproductive response) may be slowed further by lower wintertime temperatures. A number

of studies have shown that *Calanus*, for example, exhibits indicators of low feeding activity during winter (e.g., low digestive enzyme activity, reduced gut epithelium) (Tande and Slagstad, 1982; Hirche, 1983). This, however, is not universally true for all copepods. *Metridia pacifica*, for example, continued to feed at relatively high and constant levels throughout winter (Mackas and Burns, 1986).

In terms of size-fractionated mesozooplankton grazing impact, the larger mesozooplankton size fraction in our study (> 500 μm) contributed 45–82% to the total estimated grazing impact (Table 5). This would represent all but the smallest copepod species (e.g., *Oncea* spp.) and most copepod nauplii. This is consistent with observations of some but not all other investigators. For instance, Rollwagen Bollens and Landry (2000) reported the contribution of the 500–2000- μm size fraction to total grazing consistently exceeded that of the 202–500- μm size fraction. Bautista and Harris (1992) also reported that medium-sized (370–710 μm) mesozooplankton contributed > 80% of the total community (> 200 μm) grazing in temperate Atlantic waters. Bode et al. (2003) found that medium-sized copepods (500–1000 μm) contributed ca. 90% of the total annual ingestion of phytoplankton in the upwelling region off Galicia, NW Spain. Landry et al. (1994a), on the other hand, concluded that small species and developmental stages (< 1.5 mm) of mesozooplankton are some of the most important primary consumers within the mesozooplankton. This is supported by others who have reported the contributions to grazing by smaller mesozooplankton (~200–500 μm) often exceeded that

Table 5
Grazing impact of mesozooplankton (% phytoplankton consumed day⁻¹)

	Size class (µm)	Min	Max	Mean (SE)	Contribution to total (%)	Numerically dominant zooplankton taxa present (> 73 µm) ^a
Spring 2000	> 200 (total)	25.3	338.4	128.8 (31.5)		Copepod nauplii, <i>Oithona similis</i> , <i>Pseudocalanus</i> spp., <i>Acartia</i> spp.
	200–500	8.6	72.7	40.8 (12.8)	31.7	
	> 500	8.8	322.8	88.0 (28.8)	68.3	
Spring 2001	> 200 (total)	1.6	48.5	24.7 (4.6)		Copepod nauplii, <i>Pseudocalanus</i> spp. <i>O. similis</i> , <i>Microsetella rosea</i>
	200–500	1.3	29.5	7.8 (2.4)	31.7	
	> 500	0.3	41.1	16.9 (4.0)	68.3	
Spring 2002	> 200 (total)	7.0	111.9	38.3 (7.9)		Copepod nauplii, <i>Oithona similis</i> , <i>Pseudocalanus</i> spp., <i>Oncea</i> spp.
	200–500	1.4	76.3	21.1 (5.8)	55.1	
	> 500	4.3	42.9	17.2 (3.0)	44.9	
All springs (2000–2002)	> 200 (total)			60.5 (11.9)		
	200–500			23.0 (4.9)		
	> 500			37.6 (9.8)		
Winter 2002	> 200 (total)	5.0	22.7	13.4 (2.3)		Copepod nauplii, <i>Oithona similis</i> , <i>Oncea</i> spp., <i>Clausocalanus</i> spp.
	200–500	0.8	13.2	3.4 (1.4)	25.7	
	> 500	2.1	20.5	9.9 (2.1)	74.3	
Winter 2003	> 200 (total)	0.9	44.4	12.1 (4.6)		Copepod nauplii, <i>Oithona similis</i> , <i>Oncea</i> spp., <i>Clausocalanus</i> spp.
	200–500	0.1	9.8	2.2 (0.9)	17.8	
	> 500	0.3	40.2	10.0 (4.4)	82.2	
All winters (2002–2003)	> 200 (total)			12.7 (2.7)		
	200–500			2.7 (0.8)		
	> 500			9.9 (2.5)		

^aTaken from microscopic analysis of preserved ring net (> 73 µm) sample (not size-fractioned).

of larger mesozooplankton (> 500 µm) (Morales et al., 1991; Dam et al., 1995; Head et al., 1999).

Worldwide, daily mesozooplankton grazing impact can vary regionally, inter-annually and seasonally, but is generally less than 5% of the phytoplankton standing crop (range 0.10–18%) (Dagg, 1993; Dam et al., 1995; Atkinson and Shreeve, 1995). In the California Current System more specifically, daily grazing impact of chlorophyll standing stock by mesozooplankton grazers has been estimated to be ~11.7% (range 6–18%) (Landry et al., 1994b). We can not rule out the possibility that the very high grazing rates we observed in (some) springs (2000, 2002) may be biased, in part, by contamination of diatoms in our zooplankton samples although great care was taken to minimize this source of error (e.g., excluding the 73–200-µm size fraction). A more likely cause of these high mesozooplankton grazing rates includes such biological and physical factors as differences in mesozooplankton abundance, composition, phyto-

plankton composition and temperature. As such, mesozooplankton grazing had a large impact on phytoplankton standing crop, perhaps even at a rate comparable to phytoplankton growth.

Phytoplankton growth (% increase d⁻¹) was higher in spring than in winter and, during the upwelling season (spring), phytoplankton growth was higher during active upwelling periods (2001 and 2002) when larger diatoms cells were present (e.g., *Chaetoceros* sp.) than during relaxation (late bloom conditions, 2000) when the phytoplankton community was dominated by flagellates (Fig. 8). Further, phytoplankton growth was not correlated with mesozooplankton (> 200 µm) grazing impact ($R^2 = 0.01$, $n = 13$, 2000–2003). These data suggest that phytoplankton populations may be moderately reduced by mesozooplankton grazing during post-bloom conditions (2000) when phytoplankton growth rates are lower and grazing impact is higher and, conversely, less impacted during active upwelling (or bloom maturation following upwelling

events) when phytoplankton growth rates are higher and mesozooplankton grazing impact is lower. Fessenden and Cowles (1994) reported higher clearance rates of ciliates by copepods during non-bloom conditions, suggesting the important role of microzooplankton in copepod diets when phytoplankton standing crop is low (e.g., between upwelling blooms and during winter).

While not directly addressed in this study, the grazing impact of microzooplankton (<200 µm) may also play a role in mediating the transfer of primary productivity through the lower food web in the northern California upwelling system. Indeed, grazing by microzooplankton is now generally recognized to be the dominant source of mortality on phytoplankton in the open ocean (reviewed in Calbet and Landry, 2004). However, in the few instances in which microzooplankton grazing has been estimated in upwelling areas, the ratio of phytoplankton growth rates to grazing rates have ranged from ~0.5 in the Arabian Sea (Landry et al., 1998) to as high as 0.82 in the Oregon upwelling system (Neuer and Cowles, 1994). Microzooplankton grazing impact may be especially important when the phytoplankton community is dominated by smaller cells and mesozooplankton grazing impact is relatively low.

In summary, we observed that the grazing impact of mesozooplankton in this upwelling region was higher during spring than in winter, and higher during a period of relaxation (spring 2000, post-bloom) than during periods of stronger upwelling (springs 2001 and 2002). The larger (> 500 µm) size fraction contributed proportionally more to total mesozooplankton grazing impact than did the smaller (200–500 µm) size fraction. These observations point to an important, if also somewhat ephemeral, role for mesozooplankton grazers in the coastal upwelling system off northern California.

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