The potential role of microzooplankton in a northwestern Australian pelagic food web

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Abstract
The role of microzooplankton in waters adjacent to Australia’s North West Cape (21°49’S 114°14’E) was studied during the austral summers 1997/1998 and 1998/1999. We estimated microzooplankton abundance and biomass at a shallow (~20 m) shelf station and at a shelf break station (~80 m). Microzooplankton were placed into six categories: four ciliate groups (strobilidiids, strobilidiids, tintinnids, “other ciliates”), dinoflagellates, and sarcodines. Total microzooplankton abundances ranged between 0.14 × 10⁷ l⁻¹ and 3.4 × 10⁷ l⁻¹. The most abundant groups were the dinoflagellates (mean 459 ± 73 standard error l⁻¹) and strombidiids (mean 334 ± 42 standard error l⁻¹). Total microzooplankton biomass ranged between 0.03 and 1.70 g C m⁻² (mean 0.33 ± 0.05 standard error l⁻¹). Redundancy analysis indicated differences in microzooplankton community composition between stations and sampling years but no differences with sampling depth. The microzooplankton community showed considerable variability between adjacent sampling dates, reinforcing the conclusion of earlier studies that this area is a dynamic environment. Ciliate production on the shelf was estimated to be 1.05 g C m⁻² day⁻¹ (~20 mg C m⁻² day⁻¹) and 0.79 g C l⁻¹ day⁻¹ (~70 mg C m⁻² day⁻¹) at the shelf break. Ciliate production near North West Cape was two- to six-fold higher than the rate of secondary production by juvenile copepods. Despite this, ciliate grazing appears to account for only ~5% of primary production and ciliates do not appear to be a major conduit between primary producers and higher trophic levels in these waters.

Key words: Abundance, biomass, community composition, grazing impact, production

Introduction
Microzooplankton (20–200 μm; Sieburth et al. 1978) are now recognized as major grazers of phytoplankton (e.g. Calbet & Landry 2004), and they are an important component of the diet of mesozooplankton (0.2–0.14 cm), which are in turn consumed by larval fish (Hunter 1981). Furthermore, there is now growing evidence that fish larvae directly eat microzooplankton (e.g. Hunt von Herbing & Gallager 2000; Figueiredo et al. 2005). Thus, to assess larval fish recruitment there is a continued need to assess microzooplankton, and to adequately do this we must assess taxonomic composition, abundance, biomass, and production, especially in regions of the oceans where they have been hitherto ignored.

One good example of an understudied area is the northwest shelf of Australia, which is a dynamic tropical shelf system of potential larval fish recruitment. Although in these waters nutrient and phytoplankton biomass levels are typically low, and the phytoplankton are small (<5 μm), they can be moderately to highly productive on an episodic basis (1–4 g C m⁻² day⁻¹; Furnas & Mitchell 1987; Furnas submitted). In spite of this, mesozooplankton secondary production is typically low (McKinnon & Duggan 2003). We thus hypothesized that microzooplankton are an important trophic link in the waters of the northwest shelf region, and that
ciliates are important grazers of phytoplankton. However, the only existing data to test these hypotheses for northern Australian waters are from the Great Barrier Reef (Ayukai 1991) and they are probably inherently flawed due to inappropriate fixation methods. Clearly, there is a need to: (1) assess microzooplankton abundance, biomass, taxonomic composition, size structure, and productivity; (2) provide estimates of microzooplankton impacts on phytoplankton; and (3) begin to assess the biophysical attributes of the system that influence microzooplankton abundance and distribution.

To this end we examined the microzooplankton assemblage on Australia’s northwest shelf as part of a multidisciplinary effort to resolve biological oceanographic dynamics associated with recruitment processes (McKinnon & Duggan 2001, 2003; Sampey et al. 2004; Meekan et al. 2005). To provide a synoptic view of the region we chose two representative sites: one on the shelf (Station B) and one at the shelf break (Station E). Serendipitously, our sampling (summers of 1997/1998 and 1998/1999) also spanned 2 years that contrasted climatically: in 1997/1998 El Niño conditions prevailed, and there were intermittent periods of upwelling and heightened productivity (Furnas in preparation), while in 1998/1999 La Niña conditions prevailed, the mixed layer was deeper (Sampey et al. 2004) and productivity was lower (Furnas in preparation). This study, although preliminary, is the first account of microzooplankton from northwestern Australia.

Material and methods

Field sampling

Sampling occurred at ~09:00 in parallel with primary productivity experiments (Furnas in preparation), at two sites (21°49′S 114°14′E, Figure 1) from October to February in 1997/1998 and 1999/1999: Station B (~20 m depth) typified the well-mixed, episodically turbid shelf environment; Station E (~90 m depth) typified clear oceanic waters at the shelf break.

The water column structure was profiled by CTD (Seabird SBE25). Representative CTD profiles including chlorophyll fluorescence from each month and location are given in Sampey et al. (2004). Water (51 Niskin bottles) was collected at the surface (~1 m) and near the bottom (~2 m above the bottom). Our data from 1997/1998 indicated little water column stratification at Station B, and consequently in 1998/1999 we combined equal aliquots of the top and bottom samples to provide a depth-integrated composite sample. Station E was intermittently stratified in both 1997/1998 and 1998/1999, but the mixed layer was deeper in 1998/1999 (Sampey et al. 2004: Figure 2). For microzooplankton analysis, 11 samples were Lugol’s iodine fixed (8%) and stored in brown glass bottles at 6°C. For chlorophyll a analysis, 100 ml samples were filtered through 25 mm Whatman GF/F filters; the filters were frozen (~10°C) prior to fluorometric analysis (grinding in 90% acetone; Parsons et al. 1984).

Laboratory analysis

Microzooplankton samples were concentrated by settling (Gifford & Caron 2000) and then examined in settling chambers using differential interference contrast optics. Microzooplankton were placed in six categories: four ciliate groups (strombidiids, strobiliids, tintinnids, “other ciliates”), dinoflagellates and sarcodines (Figure 2); note radiolarians, acantharians, and other sarcodines were enumerated, but our sample volumes and methodologies may have been inadequate to accurately evaluate them. The trophic status of dinoflagellates (i.e. autotrophs, mixotrophs, heterotrophs) was not determined as Lugol’s iodine obscures chloroplasts, and taxonomic identification was insufficient to categorize taxa (see Discussion). All cells in the six categories were enumerated and their volume calculated from linear measurements of individual cells made using an image analysis system (Optimas 6.2), assuming standard geometric shapes for cells (Sun & Liu 2003). Tintinnid biovolume was assumed to be 21% of the lorica volume (Wilson unpublished). Biomass was estimated assuming that Lugol’s fixed cells are 70% of the volume of live cells (Wilson unpublished). Live volume was converted to carbon by the regression of Menden-Deuer & Lessard (2000) for dinoflagellates, by assuming 0.19 pg C μm⁻³ for ciliates (Putt & Stoecker 1989) and 0.0713 pg C μm⁻³ for radiolarians (Gifford & Caron 2000).

Data analysis

The maximum potential production by ciliates was estimated by calculating the maximum growth rate (μ) from ciliate biovolume and ambient temperature (Müller & Geller 1993); no equivalent relationship is available for dinoflagellates. The maximum daily amount of carbon produced was then determined for each sample as

\[ \Delta B = B_0 e^{\mu t} - B_0 \]

where \( \Delta B = \text{biomass produced} \), \( B_0 = \text{initial biomass} \), \( t = \text{time (days)} \). The daily consumption to maintain
those values of production was calculated for each sample, assuming a conservative estimate of gross growth efficiency of 10–20% (Straile 1997).

Redundancy analysis (Rao 1964) was employed to assess relationships between environmental and biotic variables. Microzooplankton abundance was examined in the context of spatial factors (station and depth), temporal factors (year and month), physical factors (temperature and salinity) and biological factors (chlorophyll a and copepod biomass). Copepod biomass was derived from cyclopoid and small calanoid copepodite biomass data from McKinnon & Duggan (2003). Because of their rarity, Radiolaria were not included in this analysis.

**Results**

**Environment**

At Station B in 1997/1998 and at both stations in 1998/1999, temperature increased during the summer, from ~23 to ~28°C (Figure 3A). This trend was not as strong at Station E in 1997/1998 and there was more variation. There was little temporal change in salinity at either station, but the salinity at Station B was marginally higher. Chlorophyll a levels tended to be highest at the beginning and end of the summer at Station B. There was little temporal change at Station E. Calanoid copepodite and cyclopoid copepod biomass (from McKinnon & Duggan 2003) tended to follow chlorophyll a levels (Figure 3B).
Microzooplankton abundance

Microzooplankton abundances ranged from $0.14 \times 10^3$ to $3.4 \times 10^3$ $l^{-1}$. The mean microzooplankton abundance at Station B was higher ($1.4 \times 10^3 \pm 0.17 \times 10^3$ standard error $l^{-1}$) than at Station E ($0.62 \times 10^3 \pm 0.06 \times 10^3$ $l^{-1}$). Dinoflagellates were generally the most abundant group (Figure 3C), and their abundance closely mirrored chlorophyll $a$ levels. Strombidiids were the next most abundant group and were more abundant than the dinoflagellates at Station B in 1998/1999; strobiliids and “other ciliates” were less abundant. Tintinnids occurred irregularly and in low abundance.

Figure 2. Representative microzooplankton taxa from North West Cape, Australia. Dinoflagellates: (A) Ceratium, (B) Ceratium, (C) Gyrodinium, (D) Proteridinium. Aloricate ciliates: (E)–(G) unidentified Strombidiid species, (H) unidentified Strobiliid species. Acantharia: (I) Tintinnids, (J) Dasytiella, (K) Parudella, (L) Eutinginnus.
Radiolarians were rare, although more common at Station E than at Station B (data not shown).

**Microzooplankton cell size**

Natural log distributions of cell volume for all taxonomic categories deviated from normality ($P < 0.001$, W–Shapiro–Wilk test statistic), were more steeply peaked than normal distributions (leptokurtic), and were positively skewed (Figure 4). Microzooplankton cell size was distributed around a median value of $\sim 1020 \mu m^3$, which corresponded to an average cell biomass of $\sim 130 \mu g$ C and an equivalent spherical diameter of $\sim 12 \mu m$. Strombidiids, tintinnids, and “other ciliates” showed the greatest degree of positive skew, and tintinnids, dinoflagellates and “other ciliates” tended to be larger (median values $= 2360, 1350$ and
Temporal differences in cell size had a substantial influence on the contribution of various microzooplankton groups to total community biomass.

**Microzooplankton biomass**

Standing stocks of dinoflagellates were greatest at Station B during the summer of 1997/1998 (Figure 5), but were the greatest contributors to microplankton biomass on all cruises. Total microzooplankton biomass (excluding the dinoflagellate component) ranged between 0.03 and 1.5 μg C l⁻¹ (mean 0.33 ± 0.05 standard error l⁻¹). No clear monthly pattern occurred during the sample period (Figure 6). Nor was there a clear trend in differences between surface and bottom samples, although there were often several fold differences (Figure 6).

**Microzooplankton community structure**

The explanatory variables employed in the redundancy analysis accounted for >60% of the total variance in microzooplankton distribution (Figure 7), with 87% of this variance explained by differences between years and 12% explained by differences between stations. Dinoflagellates were associated with high chlorophyll a concentrations, present at Station B, especially during October and January in 1997/1998 (Figures 3 and 6). Cyclopid and small calanoid copepodite biomass (from McKinnon & Duggan 2003) were also associated with high chlorophyll a levels and dinoflagellates. None of the ciliates was closely associated with copepods, chlorophyll, or dinoflagellates. Strombidiids were more abundant at Station B, as were strobilidiids and tintinnids to a lesser extent. "Other ciliates" were more evenly distributed.

**Discussion**

The biological oceanography of the North West Cape pelagic ecosystems is characterized by high variability in plankton composition and production rates between successive occupations of stations only days apart (McKinnon & Duggan 2001, 2003; Sampey et al. 2004; Meekan et al. 2005).

Figure 4. Histograms of microzooplankton biomass based on natural logs of cell volume collected from both stations during all cruises in both years. The distribution of cell volume for all taxonomic categories deviated significantly (P < 0.001, W = Shapiro–Wilk test statistic) from normality (indicated by solid line). Most cells were of a similar size (leptokurtic) with a few large individuals (positively skewed).
These studies conclude that the unpredictable nature of this region arises from complex interactions between different water masses. Briefly, local events such as upwelling (especially in 1997/1998), tidal exchange of waters from shallow waters both of Exmouth Gulf and of the northwest shelf, and mesoscale processes such as the meandering of the Leeuwin Current, all contribute to these interactions. In this work we were interested in how this variable environment influenced microzooplankton (specifically ciliates and dinoflagellates), which due to their high population growth rates may exploit episodic events, following boom–bust dynamics (e.g. Banse 1982; Montagnes 1996).

**Microzooplankton abundance and biomass**

Microzooplankton abundance was $\sim 1-2 \times 10^3 \, \text{L}^{-1}$, with dinoflagellates contributing $<50\%$, at both stations (Figure 3); these abundances are not only typical of oligotrophic tropical and subtropical systems (Table I), they are typical of the global oceans (Lynn & Montagnes 1991). In contrast, eutrophic warm water environments, such as the Northern Gulf of Mexico, may have higher microzooplankton abundance (Table I). Our abundance estimates are 10-fold higher than those of the only other available data for Australian marine waters (Ayukai 1991; Table I), suggesting that the role of
Microzooplankton may have been underestimated in that study. The tintinnid abundances reported by Ayukai (1991), in contrast, are similar to ours (~40 cells l⁻¹). These observations may be explained by the use of formaldehyde as a fixative by Ayukai (1991). Formaldehyde causes cell lysis and is a poor preservative for soft-bodied microzooplankton but not for tintinnids (Gifford 1993; Stoecker et al. 1994). In contrast, Lugol's iodine, especially at the high concentration used here, is a good preservative of microzooplankton (Stoecker et al. 1994), and we therefore consider our data to be the first good estimates of marine microzooplankton abundance in Australian waters.

The microzooplankton assemblage differed strongly between years (Figures 3 and 6), reflecting the climatic dichotomy encompassed by this study (1997/1998 El Nino vs 1998/1999 La Nina). Because we were unable to replicate this climatic factor, the generality of our observations remains to
be established by longer term datasets. There were also differences in the microzooplankton assemblage between stations (Figure 6), with lower abundances at the shelf break possibly reflecting the more oligotrophic oceanic conditions (Lynn & Montagnes 1991), although such differences are not necessarily reflected by the chlorophyll levels (Figure 3). Microzooplankton at the shallower shelf station may also have been feeding on resuspended benthic detritus and its associated bacterial microflora. Strombidiids had the strongest contribution to assemblage differences between the stations, being consistently more abundant at the shelf site (Figures 3, 5 and 6). There were no consistent differences in microzooplankton communities between depths (Figures 5 and 6) even when the water column was stratified, in contrast to the observations of previous studies in which deeper samples contained fewer microzooplankton (e.g. Pitta & Giannakourou 2000).

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The close association of copepods with potential food resources (chlorophyll, dinoflagellates) evident in the redundancy analysis (Figure 7) may be indicative of trophic linkages between them. No such linkages were evident between either copepods and ciliates or between ciliates and chlorophyll. The high correlation between dinoflagellate abundance and chlorophyll $a$ (Figure 7) may suggest that a large proportion of the dinoflagellate community was autotrophic/mixotrophic. Alternatively, but less likely, heterotrophic dinoflagellate abundance may have tracked changes in phytoplankton biomass more closely than that of other microzooplankton (primarily ciliates).

To estimate the importance of microzooplankton (including our dinoflagellate data) relative to the total food resources available to mesozooplankton and possibly larval fish, we assumed a carbon:chlorophyll ratio of 40 (Montagnes et al. 1994) and used $>10 \mu m$ chlorophyll data from Furnas (in preparation). This size range of phytoplankton is directly comparable with the microzooplankton size window described in our community analyses (average equivalent spherical diameter $=12 \mu m$; Figure 4). On average, we calculated that the total microzooplankton assemblage contributed 9% to the standing stock of potential food resources. Ciliates contributed $\sim8\%$ to the total standing stock on the shelf.
Table I. Comparison of literature values of abundance and microzooplankton biomass from subtropical/tropical waters. When biomass was not provided, values were calculated (see Material and methods), using the mean cell volumes described in Figure 4.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Abundance (l⁻¹)</th>
<th>Biomass (µg C l⁻¹)</th>
<th>Area</th>
<th>Reference</th>
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<tr>
<td></td>
<td>Mean</td>
<td>Minimum</td>
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<td>Mean</td>
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<td>Microzooplankton</td>
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<td>Ciliates (Strom + Strob + Tin)</td>
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<td>51</td>
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<tr>
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<td>0</td>
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<td>Tintinnids</td>
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H-dinoflagellates, heterotrophic dinoflagellates.

²Mean abundance and biomass from the reef face.
³Mean calculated from all cruises and all depths.
⁴Mean biomass of two cruises.
⁵Mean, minimum, and maximum of the inter-monsoonal period, and winter and summer monsoons.
⁶Abundance calculated from biomass.
⁷Mean, minimum, and maximum abundance and biomass from four cruises.
⁸"Infusoria". Assuming biomass given is wet weight, and applying a carbon conversion factor of 0.06 (McKinnon & Duggan 2003).
and 3% at the shelf break. These values suggest that on average the contribution of microzooplankton to the diet of mesozooplankton on the northwest shelf is minor.

**Potential grazing impact**

Dinoflagellates span the full range of trophic states between autotrophy and heterotrophy, including many mixotrophic forms. Our use of Lugol’s iodine had the disadvantage of obscuring chloroplasts and, therefore, preventing the classification of dinoflagellates into trophic groups. As we are more certain of the heterotrophic nature of ciliates, and there are more data on them, we have confined our calculations of grazing impact to ciliates.

Ciliate production ranged from 1.05 μg C \(\text{m}^{-2}\) \(\text{day}^{-1}\) (\(\sim 20\) mg C \(\text{m}^{-2}\) \(\text{day}^{-1}\)) at the shelf station to 0.79 μg C \(\text{m}^{-2}\) \(\text{day}^{-1}\) (\(\sim 70\) mg C \(\text{m}^{-2}\) \(\text{day}^{-1}\)) at the deeper, oceanic station. These estimates are two- to six-fold higher than those of the combined naupliar and copepodite stages of copepods measured on the same cruises (\(\sim 13\) mg C \(\text{m}^{-2}\) \(\text{day}^{-1}\); McKinnon & Duggan 2003). The method we used to estimate growth rate (Müller & Geller 1993) assumes that organisms are food replete and, therefore, these are maximum estimates, which may be unrealistically (several fold) high extrapolations. Furthermore, this method was established for organisms growing between 4 and 23°C, and temperatures in the northwest shelf often exceeded these (Figure 3). Recognizing these caveats, our maximal estimates suggest that ciliates may be important producers in these waters.

The ciliate maximum grazing impact on phytoplankton can also be estimated from production values by applying conservative estimates of gross growth efficiency of 10–20% (Straile 1997). By determining the minimum and maximum potentials of the grazing impacts (from production and gross growth efficiency ranges), we estimated that ciliates consumed a maximum of 5–10 μg C \(\text{m}^{-2}\) \(\text{day}^{-1}\) at the shelf station and 4–8 μg C \(\text{m}^{-2}\) \(\text{day}^{-1}\) at the oceanic station. Primary production estimates in the vicinity of North West Cape are \(\sim 100\) μg C \(\text{m}^{-2}\) \(\text{day}^{-1}\) at the shelf station (\(\text{^{14}C}\)-method, Furnas in preparation). Thus, on average, ciliates could consume a maximum of \(\sim 5–10\)% of this primary production. In contrast, dilution experiments conducted on our cruises, which would have included taxa other than ciliates, indicated that, on average, \(\sim 50\)% of phytoplankton production was removed by nano- and microzooplankton grazing (McKinnon unpublished). On most occasions, phytoplankton <2 μm dominate phytoplankton biomass in these waters (Furnas in preparation), and it is likely that heterotrophic nanoflagellates and dinoflagellates play a major role in consuming the balance of primary production unaccounted for by our estimates of ciliate consumption. It appears then that although the ciliates in this study were numerous and relatively small (Figures 3 and 4), and thus potential grazers of pico- and nanoplankton, on average, they would have little impact on the fate of primary production.

Strombidiids and strobilidds, which did not co-vary with their potential predators, appear to be less likely to be grazed than other similarly sized plankton. Rather than being eaten, we suggest that the evidence infers that these ciliates followed boom–bust population dynamics, recycling biomass within the water column. We base this argument on three observations. First, ciliates occurred at typical levels for pelagic ecosystems, but on average there was probably insufficient food to allow them to survive; i.e. ciliate threshold levels (the prey concentration where growth rate is zero) were 10–100 μg C \(\text{l}^{-1}\) (Montagnes 1996), and total phytoplankton biomass was \(\sim 20\) μg C \(\text{l}^{-1}\) (assuming a chlorophyll:carbon ratio of 40; Montagnes et al. 1994; Figure 3). The only means for ciliates to obtain sufficient prey would be by exploiting transient patches, which might occur temporally or spatially. Second, the abundance and biomass of ciliates varied, and the taxonomic composition varied even more, suggesting again continual shifts in species composition as ciliate populations rose and fell. Finally, as indicated above (Introduction), this is a region of episodic oceanographic and climatic events, which will stimulate rapid population dynamics of organisms such as ciliates that are capable of boom–bust dynamics over <20 days (e.g. Montagnes 1996; Montagnes & Lessard 1999). Thus, we suggest that the ciliates, which tended to be relatively small in this system, are an alternate trophic pathway for the removal of nano- and pico-autotrophic production. Rather than providing a link to upper trophic levels, these ciliates may act as a sink. Ciliate populations potentially graze down small-scale patches of prey and then die due to starvation rather than being consumed by copepods, because mesozooplankton are not capable of responding in appropriate time scales (see Montagnes & Lessard 1999).

**Conclusions**

The food web of Australia’s northwest shelf is far from adequately parameterized. Phytoplankton and dinoflagellates appear to be important components
of the diet of copepods in these waters, as occurs in many food webs, and the main link between the dominant pico-phytoplankton and copepods may be via nano-heterotrophs and dinoflagellates. We conclude that microzooplankton appear to be only a minor component of copepod diets on Australia’s northwest shelf, and reject our hypothesis that ciliates are an important component of the food web that transfers biomass to copepods and ultimately fish larvae.

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