REVIEW

Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea

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ABSTRACT: This review summarizes evidence that heterotrophic (non-pigmented, phagotrophic) dinoflagellates are often a significant component of the biomass of phagotrophic protists in the microplankton size class (20 to 200 μm), and that heterotrophic dinoflagellates are likely to be more quantitatively significant consumers of bloom-forming diatoms than copepods and other mesozooplankton. Although it has been assumed that the microzooplankton community is usually dominated by ciliates, non-pigmented dinoflagellates, including both thecate (armored forms, e.g. *Protoperdinium* spp.) and athecate gymnodinoid species, frequently compose >50 % of microzooplankton biomass, and often occur at high abundance during diatom blooms. Since phagotrophic dinoflagellates appear able to grow on diverse prey taxa and to persist at low food abundance, these protists may be able to survive during non-bloom conditions and then grow up when phytoplankton blooms occur. Heterotrophic dinoflagellates are also likely to be an important food resource for mesozooplankton. Due to fundamental differences in growth and grazing rates between phagotrophic dinoflagellates and copepods, it is vital for accurate modeling of planktonic food webs to account for grazing by both of these groups of herbivores during diatom blooms.

KEY WORDS: Microzooplankton · Heterotrophic dinoflagellates · Herbivory · Diatoms · Phytoplankton blooms · Plankton

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An association between diatom blooms and heterotrophic dinoflagellates has been noted in many environments. Feeding rate measurements have indicated that heterotrophic dinoflagellates may be significant consumers of diatom blooms.

Lessard (1991, p. 49)

INTRODUCTION

Since Landry & Hassett (1982) first proposed the dilution method to quantify the rate of consumption of phytoplankton by microzooplankton (organisms <200 μm in size) the assay has been widely used in various regions of the world ocean. The resulting data

sets have unequivocally demonstrated that in both eutrophic and oligotrophic pelagic systems, microzooplankton are quantitatively more significant grazers of phytoplankton biomass than mesozooplankton (organisms 200 to 2000 μm in size, including copepods and other metazoan grazers) (Sherr & Sherr 2002, Calbet & Landry 2004).

Although this fact is by now well-established, misconceptions remain about the roles of microzooplanktonic protists in marine food webs; two of the most common and serious being that microzooplankters mainly consume small phytoplankton cells, while mesozooplankton are the dominant grazers of phytoplankton cells ca. >20 μm in size, and that microzoo-

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planktonic protists are mainly ciliates. As an example, in a recently published diagram of a generic pelagic food web (see Fig. 2 of Rothstein et al. 2006) no trophic link is shown between protists and large phytoplankton, and microzooplankton-sized protists are labeled 'ciliates.' It has long been tacitly assumed that the community of microzooplanktonic protists is usually dominated by ciliates in terms of numbers and biomass (Ducklow 1983, Sherr & Sherr 1988, Pierce & Turner 1995, Dolan et al. 2000, Perez et al. 2000, Dolan & McKeon 2004, Vladstein et al. 2004). The group of non-ciliate protists most often recognized as potentially significant herbivores are phagotrophic nanoflagellates that consume <5 µm-sized phytoplankton (Sherr & Sherr 1992, Landry et al. 1995, Maixandeau et al. 2005).

Because ciliates and nanoflagellates are known to preferentially feed on cells of <20 µm (i.e. picoplankton and nanoplankton; Jonsson 1986, Fenchel 1987, Sherr & Sherr 1992), the assumption that the microzooplankton is dominated by these protists has led to an apparently widely held idea in the marine science community that the generally important consumers of chain-forming and large diatoms are not herbivorous protists, but copepods and other mesozooplankton. This pervasive assumption underlies statements such as that in Barber & Hiscock (2006, p. 10) regarding an iron enrichment-induced diatom bloom in the equatorial Pacific (italics added by us): '...which allows ambient diatom biomass to initially accumulate faster than ambient *mesozooplankton* can consume it (Landry et al. 2000),' even though what Landry et al. (2000) actually concluded was: 'The available data ...suggest that the accumulation of diatoms early in the bloom was as much a consequence of decreased *microzooplankton* grazing as increased diatom growth,' and '...we can surmise that the *absence* of a substantial mesozooplankton response to the patch bloom left a void that was filled by large, fast-growing protists capable of consuming and suppressing pennate diatoms.' Despite the findings of Landry et al. (2000), Barber & Hiscock (2006) presented conceptual food web diagrams depicting copepods as sole grazers of larger diatoms, and microzooplankton as consumers of only picophytoplankton and smaller protists.

The failure to recognize heterotrophic dinoflagellates as significant grazers of bloom-forming diatoms in the sea is curious, for it is 16 yr since this was first suggested by Lessard (1991). Furthermore, there have been subsequent studies demonstrating the presence of heterotrophic dinoflagellates during diatom blooms. Here, we summarize evidence showing that of the major groups of herbivores in pelagic systems, heterotrophic dinoflagellates have the greatest potential to consume large and chain forming

diatoms. Ciliates typically feed selectively at a predator-prey size ratio of 10:1 (Jonsson 1986, Fenchel 1987), while heterotrophic dinoflagellates can consume prey cells as large as themselves, or even larger (Lessard 1991, Hansen 1992, Buck & Newton 1995, Strom & Strom 1996, Jeong 1999, Jeong et al. 2004, Horner et al. 2005, Saito et al. 2006).

The main objective of this review is to provide a clearer understanding of the contribution of heterotrophic dinoflagellates to microzooplankton stocks, and of their potential grazing impacts in the sea by (1) demonstrating that heterotrophic dinoflagellates can be a significant component of the biomass of phagotrophic protists in the microzooplankton size class, and (2) summarizing evidence suggesting that heterotrophic dinoflagellates can be as significant as mesozooplankton in consuming bloom-forming diatoms. In addition, laboratory studies suggest that heterotrophic dinoflagellates are relatively non-selective feeders, and may be able to persist at low food abundance. Hence, these protists may survive during non-bloom conditions either feeding on alternative prey, or simply enduring low prey abundances until phytoplankton blooms re-occur. With the abundance of food during blooms, rapid multiplication of dinoflagellate populations can resume.

Since bloom-forming diatoms are responsible for a large part of global new/export production in the sea (Sarhou et al. 2005, Barber & Hiscock 2006), understanding the pathways of this production is of compelling interest. Although the primary fate of diatom biomass is mass sinking following bloom senescence (Smetacek 1985, Passow 1991, Turner 2002, Sarhou et al. 2005), the information summarized here suggests that the amount of bloom biomass consumed by heterotrophic dinoflagellates in the water column could be at least as great, if not greater, than that consumed by mesozooplankton. Since phagotrophic protists and copepods have fundamentally different growth and grazing responses to prey abundance, it is important to account for grazing by both of these groups of herbivores during diatom blooms.

It should be noted that many species of chloroplast-bearing dinoflagellates are also capable of phagotrophy. For example, the phototrophic dinoflagellate *Akashiwo sanguinea* (synonym: *Gymnodinium sanguineum*) was reported to consume spirotrichous ciliates (Bockstahler & Coats 1993), the photosynthetic athecate dinoflagellate *Gyrodinium instriatum* was able to prey on tintinnid ciliates (Uchida et al. 1997), and the armored phototrophic dinoflagellate *Fragilidium* cf. *mexicanum* was observed feeding on red tide and toxic dinoflagellates (Jeong et al. 1999). However, in this review we focus specifically on non-pigmented species of dinoflagellates.

REVIEW

Heterotrophic dinoflagellates are a significant component of the microzooplankton

Heterotrophic dinoflagellates have been recognized as ubiquitous in marine pelagic systems since Lessard & Swift (1985, 1986) demonstrated that about half of dinoflagellate species in marine plankton did not have chloroplasts and consumed other plankton cells. Subsequent work has confirmed that heterotrophic dinoflagellates are common in marine pelagic systems and have a potentially important role as herbivores (Lessard 1991, Hansen 1992, Lessard & Murrell 1996, Hansen & Calado 1999, Jeong 1999, Jeong et al. 2004).

In assemblages of heterotrophic dinoflagellates in marine systems, athecate dinoflagellates are typically more abundant (in both numbers and biomass) than armored dinoflagellates, which have cellulosic thecal plates (e.g. citations in Table 1, and data presented in Fig. 1B). Athecate dinoflagellates include <20 µm sized species such as the 10–12 µm *Gymnodinium* sp.

isolated from the subarctic Pacific (Strom 1991), similar to a species we observed in Georgia salt marsh estuaries (Sherr et al. 1991), and the 10–15 µm spindle-shaped dinoflagellates that are abundant during the North Atlantic spring bloom (Verity et al. 1993). Larger (>40 µm in length) athecate, heterotrophic dinoflagellates (either spindle/fusiform species such as *Gyrodinium spirale*, or round/tear-drop-shaped *Gyrodinium* spp.; Fig. 2A–C) are common under eutrophic conditions (e.g. inshore or shallow coastal habitats), or are associated with diatom blooms in the open ocean.

The results of a number of studies of biomass stocks of heterotrophic protists in the microzooplankton size range are shown in Table 1. In most of these studies, the communities of microzooplanktonic protists were categorized so that the proportional contribution of ciliates, thecate dinoflagellates and athecate dinoflagellates to total microzooplankton biomass may be determined. The results show that heterotrophic dinoflagellates often account for more than half of the total biomass of microzooplankton, although in winter and under non-bloom conditions heterotrophic dinoflagel-

Table 1. Mean $\pm$ SD total microzooplankton (MZP) protist biomass (ciliates plus heterotrophic dinoflagellates) and total heterotrophic dinoflagellate (Hdino) biomass as percent of total MZP biomass in several marine systems. –: no data

System	MZP biomass (range)	Hdino % of total MZP biomass	Athecate Hdino % of total Hdino biomass	Source
Western Arctic Ocean, bloom and non-bloom	13 $\pm$ 16 µg C l ⁻¹ (1.6–60)	60 $\pm$ 20	87 $\pm$ 13	Sherr et al. (in press)
Barents Sea	12.4 $\pm$ 3.4 µg C l ⁻¹ (9–17)	55 $\pm$ 14	–	Verity et al. (2002)
Disko Bay, Greenland, April–October	330 $\pm$ 240 mg C m ⁻² (130–760)	47 $\pm$ 14	90 $\pm$ 5	Levinsen & Nielsen (2002)
Southeast Bering Sea, bloom and non-bloom	– (9.5–133 µg C l ⁻¹)	53 $\pm$ 12	94 $\pm$ 9	Olson & Strom (2002)
Washington USA continental shelf	30 $\pm$ 15 µg C l ⁻¹ (20–52)	54 $\pm$ 12	80 $\pm$ 12	Olson et al. (2006)
Oregon USA upwelling system	6.4 $\pm$ 2.3 µg C l ⁻¹ (3–13)	54 $\pm$ 24	70 $\pm$ 17	Authors' (unpubl. data)
Northern German Wadden Sea, winter	1.2 (0–6) µg C l ⁻¹ 2.7 (0–10) µg C l ⁻¹	5 <1	40 –	Tillmann & Hesse (1998)
Northern German Wadden Sea, spring	18.1 (0–66) µg C l ⁻¹ 5.2 (0–22) µg C l ⁻¹	83 50	75 44	Tillmann & Hesse (1998)
Northern German Wadden Sea, summer	4.1 (0.1–17) µg C l ⁻¹ 12.8 (0–52) µg C l ⁻¹	69 57	20 28	Tillmann & Hesse (1998)
Kattegat, Denmark, April–October	430 $\pm$ 230 mg C m ⁻² (190–780)	63 $\pm$ 25	64 $\pm$ 32	Levinsen & Nielsen (2002)
Open North Atlantic, Spring and summer	– (0.2–2.9 µg C l ⁻¹)	50 (24–64)	–	Lessard & Murrell (1996)
Gulf of Trieste, February diatom bloom	8.4 µg C l ⁻¹	86	–	Umani & Beran (2003)
Gulf of Trieste, non-bloom	6.0 $\pm$ 0.8 µg C l ⁻¹ (5.4–6.9)	3 $\pm$ 1	–	Umani & Beran (2003)

Fig. 1. Relationship between chl *a* concentration in samples collected in the Western Arctic Ocean (●) and in the California Current System off the coast of Oregon, USA (■) and (A) heterotrophic dinoflagellates (Hdino) biomass (as a fraction of total microzooplankton [MZP, Hdino + ciliate] biomass), and (B) thecate Hdino biomass (as a fraction of total Hdino biomass). Dashed lines represent a fractional value of 0.5; for values above the line in (A), Hdino biomass comprised >50% of total MZP protist biomass, and in (B) thecate Hdino biomass comprised >50% of total Hdino biomass. Data based on inverted microscopy of Lugol-preserved samples (Sherr et al. in press and authors' unpubl. data). Briefly, 50–100 ml of Lugol-preserved (5 or 10% final volume) sample was settled for a minimum of 24 h and the whole slide was inspected by inverted light microscopy. All ciliate and heterotrophic dinoflagellate cells in each sample were counted, measured, and categorized into general taxonomic groups. In each sample inspected 200 to 600 protist cells were counted and measured. Samples preserved for epifluorescence microscopy were inspected to determine whether dinoflagellates counted in Lugol-preserved samples were hetero- or autotrophic; Hdino morphotypes were included in the microzooplankton data. The biovolume of each enumerated cell was determined using algorithms for spherical, conical, and ellipsoidal shapes. Cell biomass was estimated from biovolume using the algorithm of Menden-Deuer & Lessard (2000)

lates may compose only a small proportion of microzooplankton biomass (Table 1). The results also demonstrate that thecate heterotrophic dinoflagellates may account for a large fraction (up to 90%) of the total biomass of heterotrophic dinoflagellates.

There is additional anecdotal evidence that heterotrophic dinoflagellates are often present under conditions of high chlorophyll *a* (chl *a*) concentration, particularly during coastal diatom blooms, and that most of these dinoflagellates are gymnodinoid species (summarized in Table 2). In addition, in 2 recent studies in systems characterized by mass diatom blooms (the California Current System and the Western Arctic Ocean), we found that heterotrophic dinoflagellates composed from 20 to >80% of total microzooplankton biomass across a range of trophic states (trophic status based on chl *a* concentration) with higher proportions of heterotrophic dinoflagellates at higher phytoplankton biomass (Fig. 1A). The contribution of thecate dinoflagellates to total heterotrophic dinoflagellate biomass in these 2 systems was variable, but was generally >50% (Fig. 1B).

Heterotrophic gymnodinoid dinoflagellates as major consumers of bloom-forming diatoms

In microzooplankton communities of marine systems where diatom blooms occur, heterotrophic dinoflagellates tend to be abundant (Hansen 1991, Archer et al. 2000, Putland 2000, Olson & Strom 2002, Verity et al. 2002, Horner et al. 2005, Leising et al. 2005a). Initial focus on the ability of thecate dinoflagellates to consume bloom-forming diatoms followed demonstrations in culture that thecate non-pigmented dinoflagellates (e.g. *Protoperdinium* spp. such as the cell shown in Fig. 2D) (Jacobson & Anderson 1986, 1993, Buskey 1997), *Oblea rotunda* (Strom & Buskey 1993) and *Diplopsalis lenticula* (Naustvoll 1998) can feed on large cells (such as chain-forming diatoms) using an extruded pseudopodial membrane or pallium. However, thecate heterotrophic dinoflagellates such as *Gyrodinium* sp. also feed by direct ingestion of both large single diatom cells and diatom chains (Hansen 1992, Neuer & Cowles 1994, Li 1996, Strom & Strom 1996, Putland 2000, Horner et al. 2005, Saito et al. 2006). Putland (2000) estimated that thecate heterotrophic dinoflagellates in Logy Bay, Newfoundland, could have accounted for 38 to 61% of total microzooplankton grazing impact on spring diatom blooms. Saito et al. (2006) reported that heterotrophic *Gyrodinium* sp. increased dramatically in abundance during an iron-enriched diatom bloom (>15 $\mu\text{g chl a l}^{-1}$) dominated by *Chaetoceros debilis*; the dinoflagellates fed on diatom chains up to 12 times their own length. A mathematical model based on observed rates of grazing by *Gyrodinium* sp. suggested that the heterotrophic dinoflagellates could have grazed down the diatom bloom to ambient abundance within 7 to 8 d (Saito et al. 2006). Failure to account for the thecate component of the

Fig. 2. Large dinoflagellate morphotypes (commonly associated with diatom blooms in the western Arctic Ocean and in the Oregon upwelling system) preserved with acid Lugol solution and visualized and measured using an image analysis system consisting of a Cooke Sensicam QE CCD camera with Image Pro Plus software, mated to an Olympus BX61 Microscope. (A) Arctic Ocean, spindle- or fusiform-shaped gymnodinoid dinoflagellate with sharp cell apex, similar to *Gyrodinium spirale*; (B) Arctic Ocean, round gymnodinoid dinoflagellate with blunt cell apex; (C) Northeastern Pacific (Oregon upwelling), spindle- or fusiform-shaped gymnodinoid dinoflagellate with sharp cell apex, similar to *Gyrodinium spirale*; (D) Northeastern Pacific (Oregon upwelling), thecate heterotrophic dinoflagellate, tentatively identified as a *Protoperidinium* sp. Scale bars = 50 μm

heterotrophic dinoflagellate community in estimates of microzooplankton biomass may lead to underestimation of the potential for dinoflagellates to consume large diatoms in a particular system.

Few studies compare potential dinoflagellate and copepod grazing pressures on diatoms. We have already mentioned the results of Landry et al. (2000), which shows that microzooplankton (including large sized heterotrophic dinoflagellates) rather than mesozooplankton were the dominant consumers of an iron-enriched diatom bloom. Jeong et al. (2004) compared grazing impacts of thecate dinoflagellates (*Protoperidinium bipes*) and copepods (*Acartia* spp.) on blooms of the diatom *Skeletonema costatum* in Korean coastal waters; they estimated that at ambient abundances, the dinoflagellates could consume 0.1 to 3.4 % h^{-1} of *S. costatum* biomass, while *Acartia* spp. could remove <0.2 % h^{-1} . In a comprehensive study of

grazing on diatom blooms in Dabob Bay, Washington, USA, Leising et al. (2005a,b,c) found that microzooplankton (dominated by large gymnodinoid dinoflagellates) were the major grazers of diatoms and that copepod herbivory had much less impact on bloom diatoms. In fact, selective consumption of microzooplankton herbivores by copepods could relieve grazing pressure on diatoms.

Heterotrophic gymnodinoid dinoflagellates can consume and grow on a wide range of prey

Several studies report feeding and growth rates of phagotrophic dinoflagellates, although most of these have been based on growth and grazing rates of cultured monospecific isolates. Gymnodinoid dinoflagellates have a wide range of prey types and sizes (e.g. Lessard 1991, Hansen 1992, Nakamura et al. 1995a, Jeong 1999). Small (<20 μm) gymnodinoid dinoflagellates feed on coccoid cyanobacteria (Strom 1991) and on small (2–5 μm) eukaryotic phytoplankton (Sherr et al. 1991). Larger species of gymnodinoid dinoflagellates feed and grow on a wide variety of prey types, including individual taxa of phytoflagellates and centric diatoms ranging in size from 7 to 50 μm in equivalent spherical diameter (Hansen 1992), the

red tide ochrophyte *Chattonella antiqua* (Nakamura et al. 1992), the red-tide dinoflagellates *Prorocentrum minimum* (Kim & Jeong 2004) and *Gymnodinium miki-motoi* (Nakamura et al. 1995b), the harmful raphidophyte *Heterosigma akashiwo* (Jeong et al. 2005), diverse phytoflagellates (Nakamura et al. 1995a, Tang & Simó 2003) and heterotrophic nanoflagellates (Jeong et al. 2007). This last report supports the observation of Lessard & Rivkin (1986) that athecate heterotrophic dinoflagellates consume either bacterioplankton or bacterivores during early spring in Antarctic waters.

Survival of dinoflagellates at low prey abundance

Although some species of dinoflagellate are known to form cysts when food concentrations fall below a critical threshold (Goodman 1987), gymnodinoid

Table 2. Reports of heterotrophic dinoflagellates, with emphasis on gymnodinoid dinoflagellates, in various oceanic regions

Region	Comments	Source
Polar		
Weddell Sea, Southern Ocean	Heterotrophic <i>Gymnodinium</i> sp. suggested to be important herbivores in the Weddell Sea	Bjørnsen & Kuparinen (1991)
East Antarctica, Southern Ocean	<i>Gyrodinium</i> sp. abundant and important herbivore	Archer et al. (1996)
Canadian Arctic	Heterotrophic <i>Gyrodinium</i> spp. observed to feed on diatoms	Bursa (1961)
Disko Bay, Greenland	Heterotrophic dinoflagellate biomass dominated by athecate species, mainly gymnodinoids	Nielsen & Hansen (1995), Levinsen & Neilsen (2002)
Disko Bay, Greenland	During diatom blooms, heterotrophic dinoflagellates averaged 70 % of integrated microzooplankton biomass	Levinsen et al. (1999)
Barents Sea	Heterotrophic dinoflagellates coincident with diatoms	Verity et al. (2002)
Western Arctic Ocean	Athecate heterotrophic dinoflagellates, including <i>Gyrodinium</i> spp, composed 20 to 88 % of total microzooplankton biomass, and were most abundant during diatom blooms	Sherr et al. (in press)
Sub-Arctic		
Subarctic Northwest Pacific Ocean	Large heterotrophic <i>Gyrodinium</i> spp. were major grazers of an iron-enrichment-induced diatom bloom	Saito et al. (2006)
Shelikof Strait, Alaska	Heterotrophic dinoflagellates dominated the microprotozoan assemblage during the spring diatom bloom	Howell-Kubler et al. (1996)
Bering Sea	Increase in biomass of <i>Gyrodinium</i> spp. paralleled increase in biomass of large phytoplankton	Olson & Strom (2002)
Southeastern Bering Sea	Heterotrophic dinoflagellates (Hdino) were greater contributors to microzooplankton biomass than were ciliates (Cil), with an average ratio of 2.3 Hdino:Cil	S. Strom & K. Fredrickson (unpubl. data)
Coastal Gulf of Alaska	Gymnodinoid forms dominated the dinoflagellates; at stations with diatom blooms, dinoflagellates were twice as abundant as ciliates	Liu et al. (2005)
Newfoundland coastal waters	<i>Gymnodinium</i> spp. composed ca. 80 % of total dinoflagellates counted during the spring diatom bloom	Putland (2000)
Temperate coastal		
Kattegat, Denmark	Athecate heterotrophic dinoflagellates (including <i>Gyrodinium spirale</i>) important herbivores in pelagic food webs	Hansen (1991, 1992) Levinsen & Neilsen (2002)
Northern German Wadden Sea	Athecate heterotrophic dinoflagellates, such as <i>Gymnodinium heterostitatum</i> , fed on <i>Phaeocystis</i> cells	Tillmann & Hesse (1998)
West coast of Sweden	<i>Gyrodinium</i> cf. <i>spirale</i> increased exponentially after the peak of the spring bloom and was able to control further diatom growth	Tiselius & Kuylensstierna (1996)
Narragansett Bay, Rhode Island, USA	A <i>Gyrodinium</i> sp. isolated from the Bay was found to consume diatoms and grow in culture	Li (1996)
Harbor of Alexandria, Egypt	>50 µm sized cells (including <i>Gyrodinium fusiforme</i>) contributed >90 % of the biomass of heterotrophic dinoflagellates	Ismael (2003)
Gulf of Trieste, Northern Adriatic Sea	<i>Gyrodinium</i> spp. dominated the community of heterotrophic dinoflagellates from November to May	Umani & Beran (2003)
Korean coastal waters	<i>Gyrodinium dominans</i> and <i>G. spirale</i> consumed a red-tide dinoflagellate and grew	Kim & Jeong (2004)
Dabob Bay, Puget Sound, Washington	<i>Gyrodinium spirale</i> was a major contributor to microplankton carbon and consumed diatoms	Horner et al. (2005)
Coastal Pacific Ocean off Washington	80 % of heterotrophic dinoflagellate biomass was composed of athecate species; highest clearance rates by <i>Calanus pacificus</i> were on heterotrophic gymnodinoid dinoflagellates	Olson et al. (2006)
Oregon upwelling system	Gymnodinoid dinoflagellates were most abundant during the upwelling season, often exceeding the biovolume of ciliates and of thecate dinoflagellates. Rates of herbivory were closely linked to the abundance of this group of dinoflagellates. The abundance of large-celled gymnodinoids (>20 µm) and large phytoplankton (>20 µm, mostly diatoms) covaried, indicating that the bloom-forming diatoms were being utilized as a food source	Neuer & Cowles (1994)

Table 2 (continued)

Region	Comments	Source
Mejillones Bay Chile upwelling system	Heterotrophic dinoflagellates were the major grazers of large diatoms, and were a food resource for copepods	Vargas & Gonzalez (2004)
Temperate/subtropical open ocean		
North Atlantic Ocean	50 % of dinoflagellate species were heterotrophic	Lessard & Swift (1986)
North Atlantic Ocean	Spindle-shaped heterotrophic <i>Gyrodinium</i> sp. 10–15 µm in length were abundant and grazed <5 µm phytoplankton	Verity et al. (1993)
Gulf of Mexico	<i>Gyrodinium</i> spp. were an important component of the microzooplankton and were observed to ingest chain-forming diatoms	Strom & Strom 1996)
Eastern equatorial Pacific IronEx II	Grazing impact of larger protists, dinoflagellates and ciliates >20 µm in size, was especially apparent at the peak of the iron induced patch bloom of large pennate diatoms, when a balance between growth and grazing appears to have been achieved	Landry et al. (2000)
Bay of Bengal and the Andaman Sea	Heterotrophic dinoflagellates averaged 59 %, and were as high as 80 %, of total microzooplankton biomass	Jyothibabu et al. (2003)
Indian Ocean	The dinoflagellate community was dominated by athecate species, e.g. <i>Gyrodinium spirale</i> , <i>G. dominans</i> , <i>G. glaucum</i>	Nielsen et al. (2004)

dinoflagellates isolated from marine pelagic habitats do not encyst in culture (Hansen 1992). Heterotrophic dinoflagellates may adapt to low prey abundance by reducing metabolic rate when they have stopped growing. Reduction in the rate of respiration in starving protists (in comparison with actively growing cells) has been demonstrated in a number of laboratory experiments with isolated species (Fenchel & Finlay 1983). Both thecate and athecate species of heterotrophic dinoflagellates persist in the absence of prey. Survival of the thecate dinoflagellate *Protoperdinium depressum* for up to 71 d at <1 µg C l⁻¹ of diatom biomass was likely due to a reduction in the dinoflagellate's metabolic rate (Menden-Deuer et al. 2005). Hansen (1992) found that when moderately starved cells of *Gyrodinium spirale* were completely deprived of prey, they persisted for 48 h with minimal decrease in abundance. Jakobsen & Hansen (1997) reported that under starvation conditions, the heterotrophic dinoflagellate *Gymnodinium* sp. survived for a longer time than the ciliate *Balanion comatum*. At high densities in laboratory culture (10³ to 10⁴ cells ml⁻¹), phagotrophic dinoflagellates may resort to cannibalism when biomass of other prey is low (e.g. Jeong & Latz 1994); however, at the low cell abundances of heterotrophic dinoflagellates *in situ* (<1 to 100 ml⁻¹), it is less likely that cannibalism plays a role in survival.

Other roles of heterotrophic dinoflagellates in marine pelagic systems

In addition to their role as herbivores in marine systems, ciliates and heterotrophic dinoflagellates in the

microzooplankton serve as a quantitatively and qualitatively significant food resource for mesozooplankton (Stoecker & Capuzzo 1990, Kleppel 1993, Suzuki et al. 1999, Levinsen et al. 2000, Vincent & Hartmann 2001, Leising et al. 2005b,c, Liu et al. 2005, Olson et al. 2006, Campbell et al. in press). Due to their cell size and biochemical composition, microzooplanktonic protists are often preferred food for copepods, and feeding on microzooplankton along with phytoplankton can enhance copepod fecundity (Kleppel 1993, Klein Breteler et al. 1999, Bonnet & Carlotti 2001, Castellani et al. 2005).

Athecate heterotrophic dinoflagellates have been identified as a significant food resource for mesozooplankton (Stoecker & Capuzzo 1990, Suzuki et al. 1999, Levinsen et al. 2000, Vincent & Hartmann 2001, Leising et al. 2005b,c, Liu et al. 2005, Olson et al. 2006). Suzuki et al. (1999) found that heterotrophic gymnodinoid dinoflagellates were cleared by *Paracalanus* sp. at much higher rates than ciliates in the Seto Inland Sea, Japan. During diatom blooms in the Gulf of Alaska, heterotrophic dinoflagellates were a more important component of the diet of the copepod *Neocalanus cristatus* than were ciliates (Liu et al. 2005). Leising et al. (2005b,c) reported that large gymnodinoid dinoflagellates formed a variable but often important component of the diet of copepods in Dabob Bay, Washington, and Olson et al. (2006) found that heterotrophic gymnodinoid dinoflagellates were preferred prey for copepods off the coast of Washington state, USA.

Consumption of diatoms by heterotrophic dinoflagellates (both thecate and athecate species) also has implications for biogeochemical cycles. In the process of feeding on diatoms, pallium-feeding thecate

dinoflagellates discard empty silica frustules (Jacobsen & Anderson 1986), while athecate dinoflagellates that directly ingest diatoms produce mini-fecal pellets composed of frustules with little associated carbon (Buck & Newton 1995, Strom & Strom 1996, Horner et al. 2005, Saito et al. 2006). The production of these pellets uncouples the sinking flux of diatom silica and carbon, speeding up the dissolution rate of frustules. In addition, heterotrophic dinoflagellate grazing contributes to recycling of inorganic nitrogen and phosphorus via excretion of dissolved and particulate materials, in addition to the nutrient regeneration due to heterotrophic bacteria, bacterivorous flagellates, other herbivorous protists, and metazoans (Caron & Goldman 1990, Dolan 1997, Kirchman 2000).

CONCLUSIONS

Based on the observations summarized above, we propose that herbivorous dinoflagellates, especially athecate gymnodinoid forms, are the component of the microzooplankton with the greatest impact on bloom-forming diatoms. Ciliates have not been shown to effectively feed on large or chain-forming diatoms, and thecate dinoflagellates such as *Protoperdinium* spp., in general, are less abundant than athecate dinoflagellates during diatom blooms. In addition, the broad prey spectrum of gymnodinoid dinoflagellates and their ability to persist under conditions of low prey abundance suggest that these protists may be able to survive under a wide range of conditions in the sea, and thus be positioned to quickly increase to high abundance during diatom blooms (as observed by Saito et al. (2006) during an iron-enrichment-induced bloom).

Failure to accurately conceptualize the major trophic pathways of marine food webs has implications for the success of future research programs and modeling efforts. If heterotrophic dinoflagellates are not included in analyses of microzooplankton, plankton food web models incorporating microzooplankton growth and grazing scaled to field-measured biomass stocks would seriously underestimate this (the microzooplankton) component of the plankton community. In many previous studies of microzooplankton herbivory, ciliates were the only grazing protists enumerated (Dolan & McKeon 2004).

One reason for the failure to include dinoflagellates in assessments of microzooplankton communities is that the 'gold standard' for preservation and enumeration of large protists, i.e. acid Lugol fixation followed by inverted microscopy (Utermöhl 1931), precludes identification of chloroplasts in protistan cells. Thus, it is not easy to distinguish strictly heterotrophic from autotrophic dinoflagellates using this approach. Epi-

fluorescence microscopy allows discrimination of these types of dinoflagellates. However, in our experience, heterotrophic dinoflagellates are not adequately enumerated by settlement on filters, due to lysis of a variable fraction of athecate forms during aldehyde preservation and filtration. One approach to dealing with this problem is preparation and inspection of paired subsamples, one preserved with 5 to 10% final concentration acid Lugol's solution, and the other preserved with aldehyde fixative, stained with a fluorochrome such as DAPI, settled onto membrane filters and stored frozen until inspection via epifluorescence microscopy (Sherr & Sherr 1993). In this way, quantitative counts can be made via the Utermöhl method, and morphological types of dinoflagellates that are observed in a Lugol-preserved sample can be checked for presence or absence of chloroplasts in a corresponding sample prepared for epifluorescence microscopy.

It is clear that the contribution of dinoflagellates to the stocks and rate processes of microzooplankton can no longer be discounted in studies of the structure and functioning of marine pelagic food webs. We urge that in future research efforts, stocks and grazing impacts of phagotrophic dinoflagellates (including thecate and athecate species) be assessed, and that conceptual and simulation models of pelagic food webs explicitly include the potentially major trophic link between these protists and bloom-forming diatoms.

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