Chapter 10

DIVERSITY AND DISTRIBUTIONS OF TINTINNIDS

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10.1 INTRODUCTION

The diversity and distributions of planktonic organisms are a subject that has intrigued oceanographers for well over a century. Early observations emphasized the differences in species assemblages that characterize different areas, perhaps corresponding to different water masses. For example, by the early 1900s the distinct character of the polar compared with temperate assemblages in both hemispheres was recognized as well as the similarity of the polar assemblages. These findings led to the suggestion that perhaps undercurrents joined the polar seas (e.g. Cleve 1900). Seasonal changes in the species found in coastal systems were also well known. Seasonality, first attributed to changes in changes in currents and water masses, was shown to likely result from shifts in local conditions of light, temperature, and nutrients (e.g. Brandt 1905). Today, the distributional patterns of planktonic organisms remain an area of very active research because, even though some patterns can be documented from space, such as those of phytoplankton, identifying the factors controlling their dynamics remains elusive (see, for example, Kudela 2010).

This chapter explores the biogeography and patterns of species diversity of tintinnids. The basic geographic assemblages and patterns are defined. Seasonal changes of tintinnid assemblages of coastal systems are documented and the relationships between abundance and distribution both temporal and spatial are examined. When possible, the patterns of tintinnids are compared with those of other groups of planktonic organisms.

10.2 BIOGEOGRAPHY

Global biogeography

The first attempt to quantify large-scale ciliate distributions was by Entz (1884), who tabulated presence/absence of each species of the known catalogue of marine planktonic species, calculating a percentage of total species for each sea. Not surprisingly, he found that Northern European waters, from which most species had been described, appeared the most species-rich. The distributions presented here are also based on simple species records but of a considerably larger database than that available to Entz. The tintinnid distributions are an updated version that of Pierce &
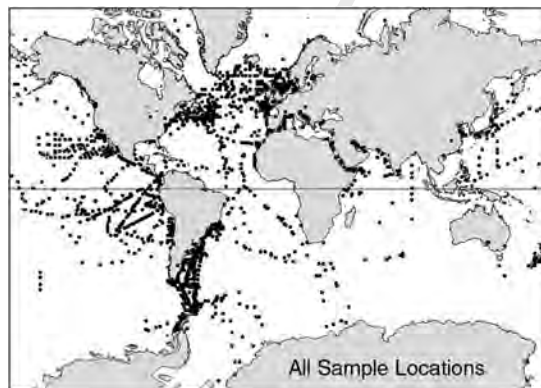
Fig. 10.1 The 1800 locations of tintinnid species records used to map distributions.

Turner (1993), increased to include 302 references, 1800 sampling locations, and references up to the year 2011. This has yielded a fairly extensive geographic coverage (Fig. 10.1).

The distributions are based on literature reports of species occurrences. Data recorded were species names along with latitude and longitude of sample collection as reported, or determined from sample site names, or maps in the report. The references are indicated in the reference list with an asterisk. The database was used to plot occurrences on world maps for each genus that met a minimum occurrence criterion of containing a species reported in at least four publications by two different authors. Here, the term "species" in relation to distributional patterns refers to morpho-species.

The relationship between morpho-species and the generally accepted biological definition of "species" in ciliates is very far from clear as morphology, mating types, and genetics can be discordant (Hall & Katz 2011). However, although data are very limited at present, it does suggest that at least in terms of genetics, morpho-species of tintinnids, rather than grouping cryptic species, may more often be different phenotypes of the same genetic species. First, it appears that geographically distant populations of planktonic ciliates can be genetically identical (Agatha et al. 2004a; Katz et al. 2005). Thus there is *a priori* no reason to associate geographic separation in species of planktonic ciliates with genetic isolation. Secondly, although genetic studies of tintinnid are very sparse, identical sequences have been found for different "species" of *Tintinnopsis* (Li et al. 2009) *Petalotricha* and *Cyttarocylis* (Bachy et al. 2012) as well as *Favella* (Kim et al. 2010). Recently some

Table 10.1 Biogeographic distribution patters of common tintinnid genera; genera considered were those that included species reported in at least four publications by two different authors.

Cosmopolitan	Neritic	Warm water	Boreal	Austral
Acanthostomella	*Favella*	*Amplectella*	*Parafavella*	*Cymatocylis*
Amphorellopsis	*Helicostomella*	*Ascampbelliella*	*Ptychocylis*	*Laackmanniella*
Amphorides	*Leprotintinnus*	*Brandtiella*		
Codonella	*Metacylis*	*Canthariella*		
Codonellopsis	*Stenosemella*	*Climacocylis*		
Dadayiella	*Stylicauda*	*Codonaria*		
Dictyocysta	*Tintinnidium*	*Cyttarocylis*		
Eutintinnus	*Tintinnopsis*	*Daturella*		
Parundella		*Epicancella*		
Protorhabdonella		*Epiplocylis*		
Salpingacantha		*Epiplocyloides*		
Salpingella		*Petalotricha*		
Steenstrupiella		*Poroecus*		
		Proplectella		
		Rhabdonella		
		Rhabdonellopsis		
		Undella		
		Undellopsis		
		Xystonella		
		Xystonellopsis		

ambiguities in establishing species boundaries have been found (Santoferrara et al. 2012, Xu et al. 2012), but no cryptic species have been discovered so far.

We largely follow the tintinnid genus distributions established by Pierce & Turner (1993): cosmopolitan, neritic, warm–temperate, boreal, and austral. These distributional patterns, or categories, have long been known to characterize many if not most groups of planktonic organisms (see, for example, Backus 1986), including well-studied protist groups such as foraminifera (see, for example, Bé & Tolderlund 1971). As Taylor (1987) stated for marine dinoflagellates, "The essence . . . is a modified latitudinal cosmopolitanism: the occurrence of the same (morpho-) species around the world within broad latitudinal limits, the boundaries of which approximate to particular upper-layer temperatures." Within the broad latitudinal bands, neritic or coastal forms can be distinguished from oceanic species among dinoflagellates (Taylor 1987) and the same large-scale patterns characterize diatoms as well (Guillard & Kilham 1977).
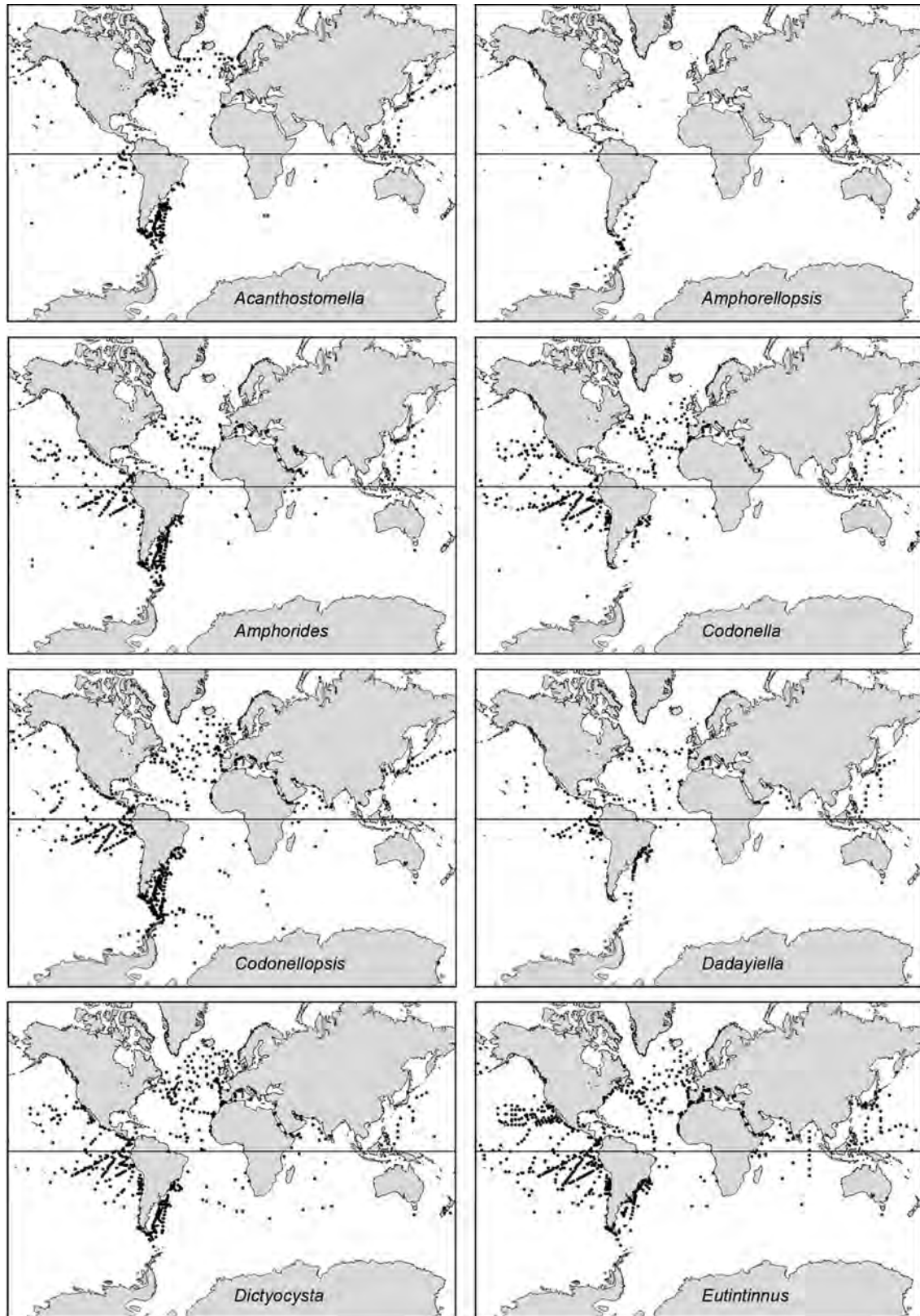
Cosmopolitan

We designate as "cosmopolitan" those genera containing species recorded from the Arctic, through the

Tropics and into the Southern Ocean, and not restricted to nearshore areas (Figs 10.2 and Fig. 10.3). Most, but not all, of the genera are forms that have purely hyaline loricae. The exceptions are the genera *Acanthostomella*, *Dictyocysta*, *Codonella*, and *Codonellopsis*, all of which include "agglutinating species". However, the particles used by species of these genera are mainly remains of diatoms and coccolithophorids, which are also quite widespread in the world ocean.
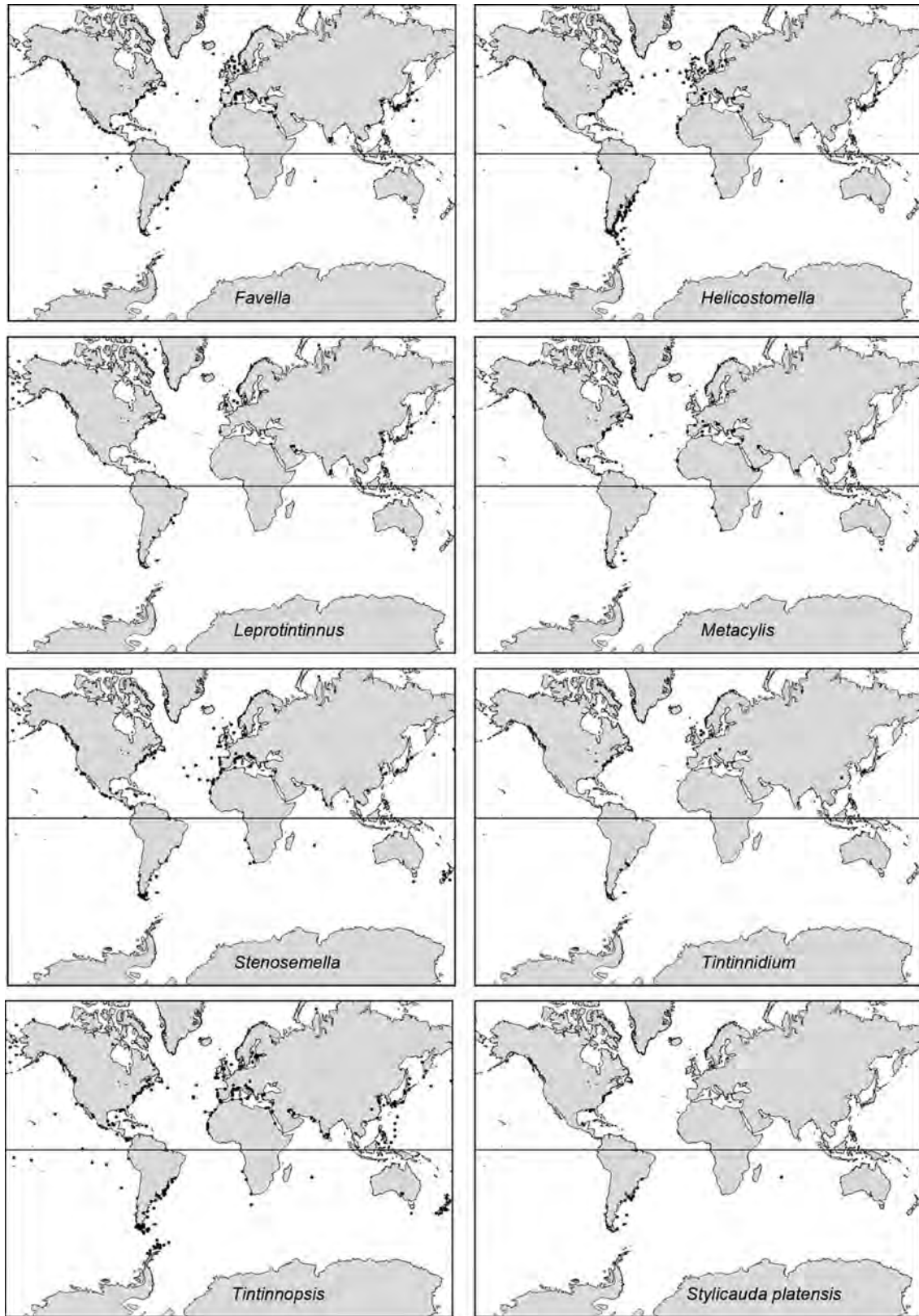
Neritic

We define neritic genera as those containing species that are very largely restricted to nearshore waters (Fig. 10.4). These are the most familiar forms as field-work has usually focused on nearshore environments and most laboratory studies have used species from coastal waters. Neritic genera are a morphologically heterogeneous set including both genera formed of species with agglutinated loricae (*Tintinnopsis*, *Tintinnidium*, *Stenosemella*, *Leprotintinnus*, *Stylicaudata*) as well as genera with hyaline loricae (*Metacylis*, *Helicostomella*, *Favella*). The size range of species is also very large including some of the largest tintinnids known (*Favella* spp.) and the smallest (*Tintinnopsis* spp.). The genera all occupy a nearly pole-to-pole latitudinal

Fig. 10.2 The cosmopolitan distributions of the genera *Acanthostomella*, *Amphorellopsis*, *Amphorides*, *Codonella*, *Codonellopsis*, *Dadayiella*, *Dictyocysta*, and *Eutintinnus*. Species of these genera have been reported from neritic and oceanic areas from Arctic to Antarctic waters.
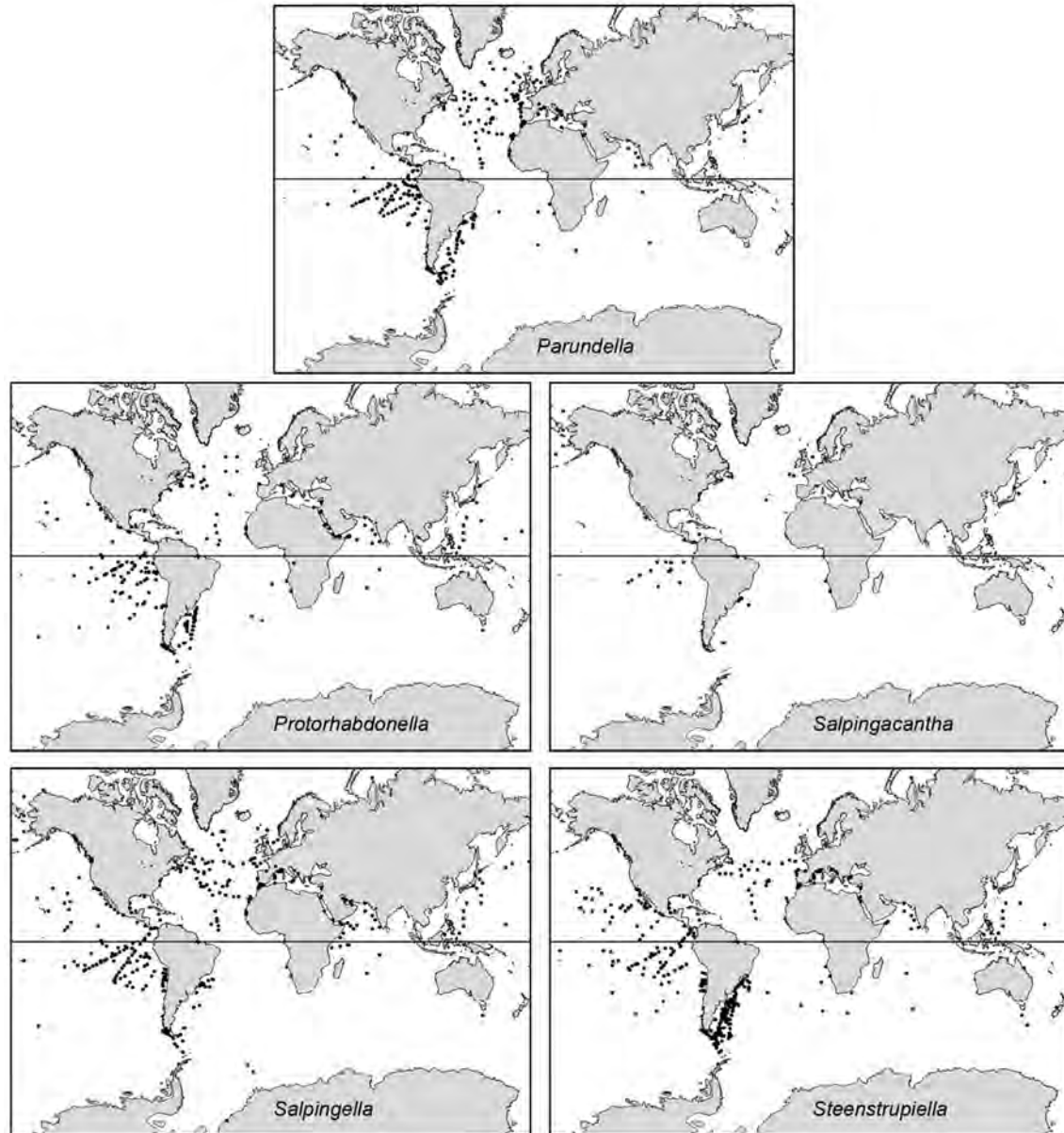
Fig. 10.3 The cosmopolitan distributions of the genera *Parundella*, *Protorhabdonella*, *Salpingacantha*, *Salpingella*, and *Steenstrupiella*. Species of these genera have been reported from neritic and oceanic areas from Arctic to Antarctic waters.

Fig. 10.4 Neritic distributions characterize species of the genera *Favella*, *Helicostomella*, *Leprotintinnus*, *Metacylis*, *Stenosemella*, *Tintinnidium*, *Tintinnopsis*, and *Stylicaudata*. Although some records are from open waters, most species records are from coastal waters.

distribution; thus the limit is to coastal waters, rather than a temperature zone.

The restriction of the genera *Tintinnopsis*, *Stenosemella*, and *Tintinnidium* to nearshore areas probably reflects a requirement for small mineral particles used to form loricae in all three genera. Waters with sufficient concentrations of small mineral particles are likely limited to areas that are relatively shallow and turbulent. The restriction of the forms with hyaline loricae (*Favella*, *Helicostomella*, and *Metacylis*) to coastal waters is difficult to explain. Cyst formation is known in species of *Favella*, *Helicostomella*, and *Leprotintinnus* (Reid & John 1978); it may be that a cyst stage is an important component in their life cycles, restricting distribution to shallow waters.

Warm–temperate

Warm–temperate genera are those observed in both coastal systems and open waters throughout the world ocean (Figs 10.5–10.7). This group differs from cosmopolitan only in that species of these genera are absent from sub-polar and polar waters. It is the largest biogeographic group in terms of the number of genera and species. Although their distributions are nearly cosmopolitan, many of the genera such as *Brandtiella*, *Xystonellopsis*, *Codonaria*, and *Climacocylis* are characteristic of tropical and sub-tropical waters and are rarely reported from temperate waters. None of the genera contains species with agglutinated loricae.

Boreal

The genera *Parafavella* and *Ptychocylis* (Fig. 10.8) have long been known to be restricted to Arctic and Subarctic waters. Notably, species of both *Parafavella* and *Ptychocylis* appear to produce loricae that are variable in overall length and shape but consistent in oral diameter (Burkovsky 1973; Davis 1978, 1981). Both genera comprise species with relatively large oral diameters of about 50 μm, suggesting exploitation of similar-sized prey.

Austral

The genera *Cymatocylis* and *Laackmanniella* (Fig. 10.9) are restricted to Antarctic and Subantarctic waters. In common with boreal genera, species of both *Cymatocylis* and *Laackmanniella* have variable lorica characteristics, especially length. Unlike the boreal genera, the two austral genera group species of distinctly different

oral diameters. *Cymatocylis* species average about 100 μm whereas *Laackmanniella* species have considerably smaller oral diameters of 30–35 μm, indicating that likely different-sized prey are exploited by *Cymatocylis* and *Laackmanniella* spp.

Distributions of commonly reported species

Although the cosmopolitan genera contain the most common species, none of the individual species within the genera is cosmopolitan. For example, the most widespread species of *Acanthostomella*, *A. norvegica*, appears to be excluded from warm waters (Fig. 10.10). The distribution of *A. norvegica* is reminiscent of the "bi-polar" distribution known among a wide range of planktonic taxa, for example radiolaria and medusozoa (Stepanjants et al. 2006) as well in foraminifera (Bé & Tolderlund 1971; Darling et al. 2004) and dinoflagellates (Montresor et al. 2003). In the specific cases of the foraminfera *Neogloboquadrina pachyderma* and the dinoflagellate *Polarella glacialis*, there is evidence of genetic differentiation between the northern and southern populations (Darling et al. 2004; Montresor et al. 2003). This may be the case for *A. norvegica* but it has yet to be examined.

Globally, the four most widely distributed and most-often reported species are *Amphorides quadrilineata*, *Dadayiella ganymedes*, *Eutintinnus apertus*, and *Steenstrupiella steenstrupii*. These species have been reported both from neritic and open waters yet appear to be absent from far northern and southern seas (Fig. 10.10). Thus, there appears to be no species that is truly cosmopolitan. Furthermore, within cosmopolitan genera there are species that, though frequently reported, have restricted distributions and appear to be endemics. For example, among *Codonellopsis* species, *C. lagunela* is found only in the North Atlantic, *C. gaussi* only in the Southern Ocean, whereas *C. ecuadata* has been recorded only from the Indian and tropical Pacific Oceans (Fig. 10.11). These species of *Codonellopsis* are rather large and distinctive, so it is unlikely that they were frequently overlooked or mistaken for other species.

General considerations in global biogeography of tintinnids

It should be noted that there are, in principle, opposing views on the biogeography of protists in general. One posits no protist biogeography: "everything is
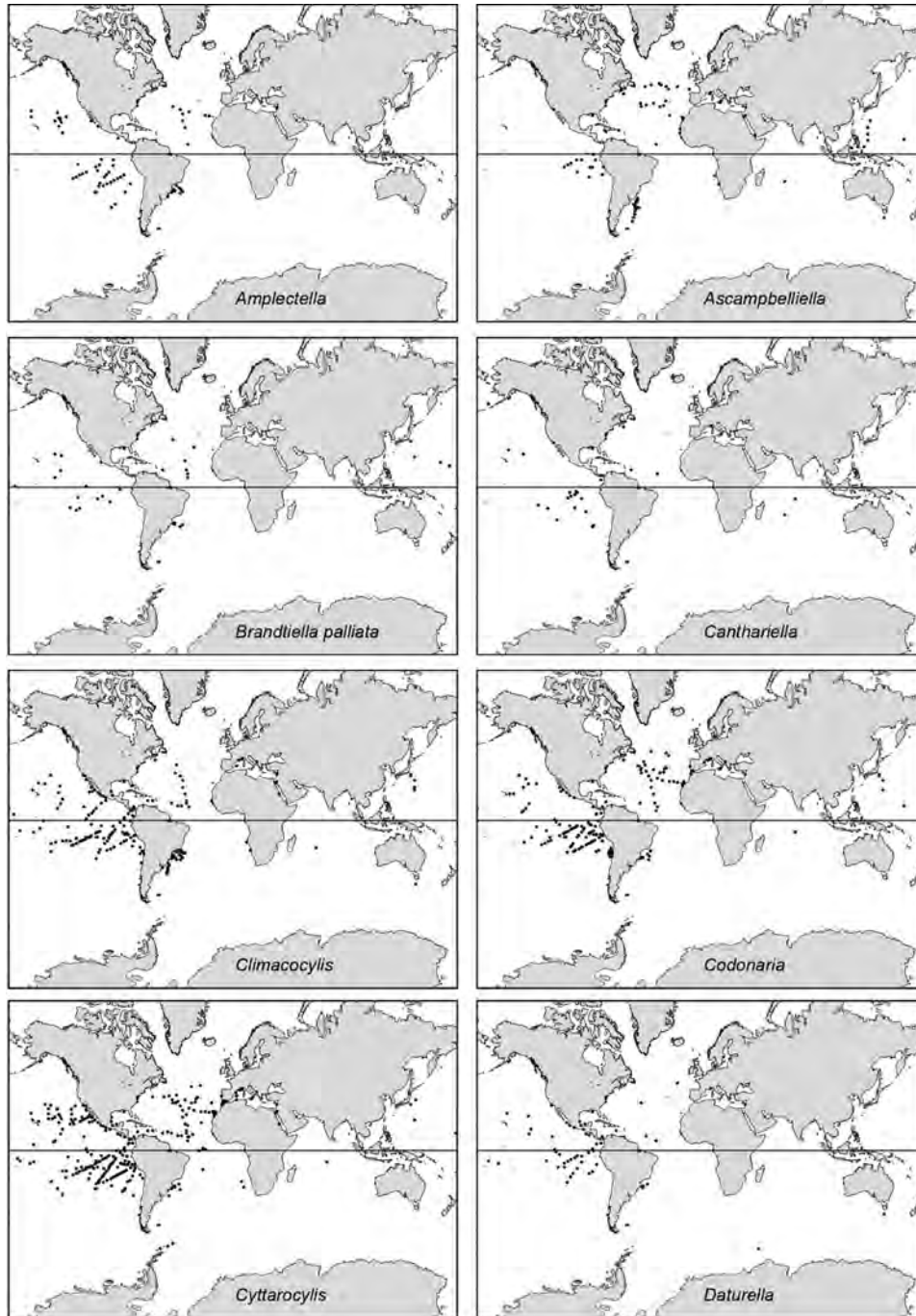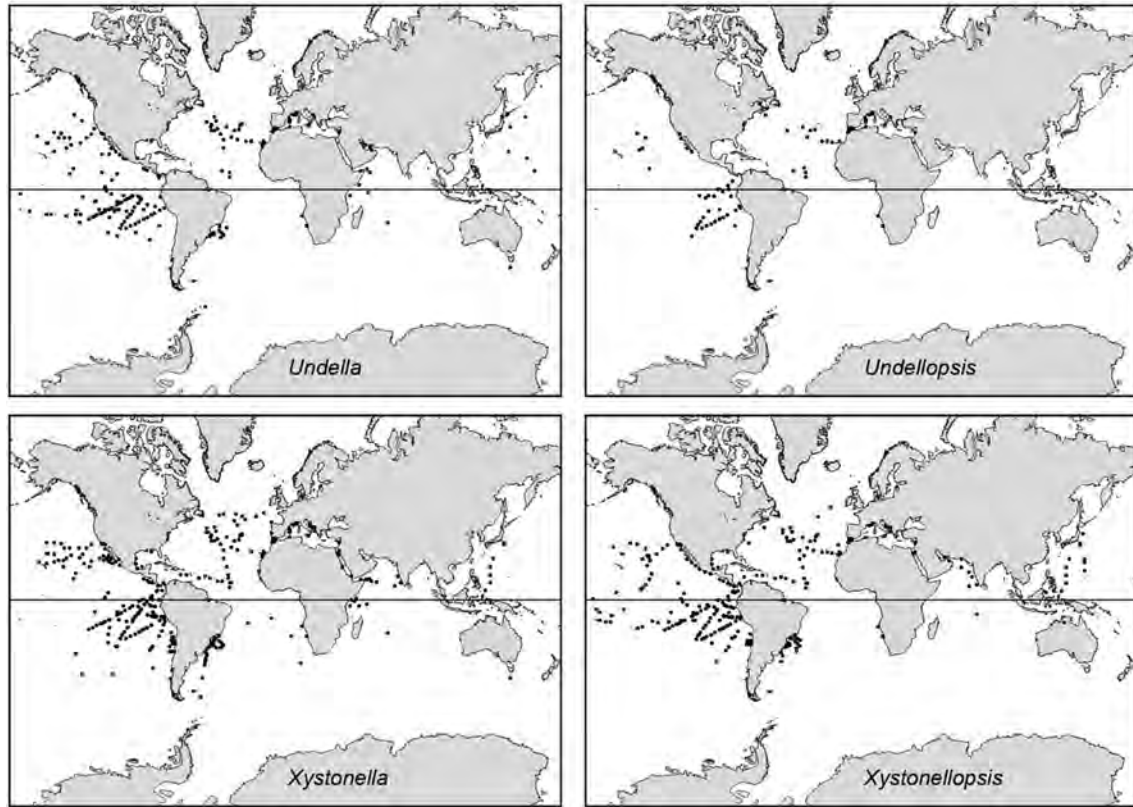
Fig. 10.5 Warm–temperate distributions are shown by *Amplectellopsis, Ascampbelliella, Brandtiella, Canthariella, Climacocylis, Codonaria, Cyttarocylis,* and *Daturella.*
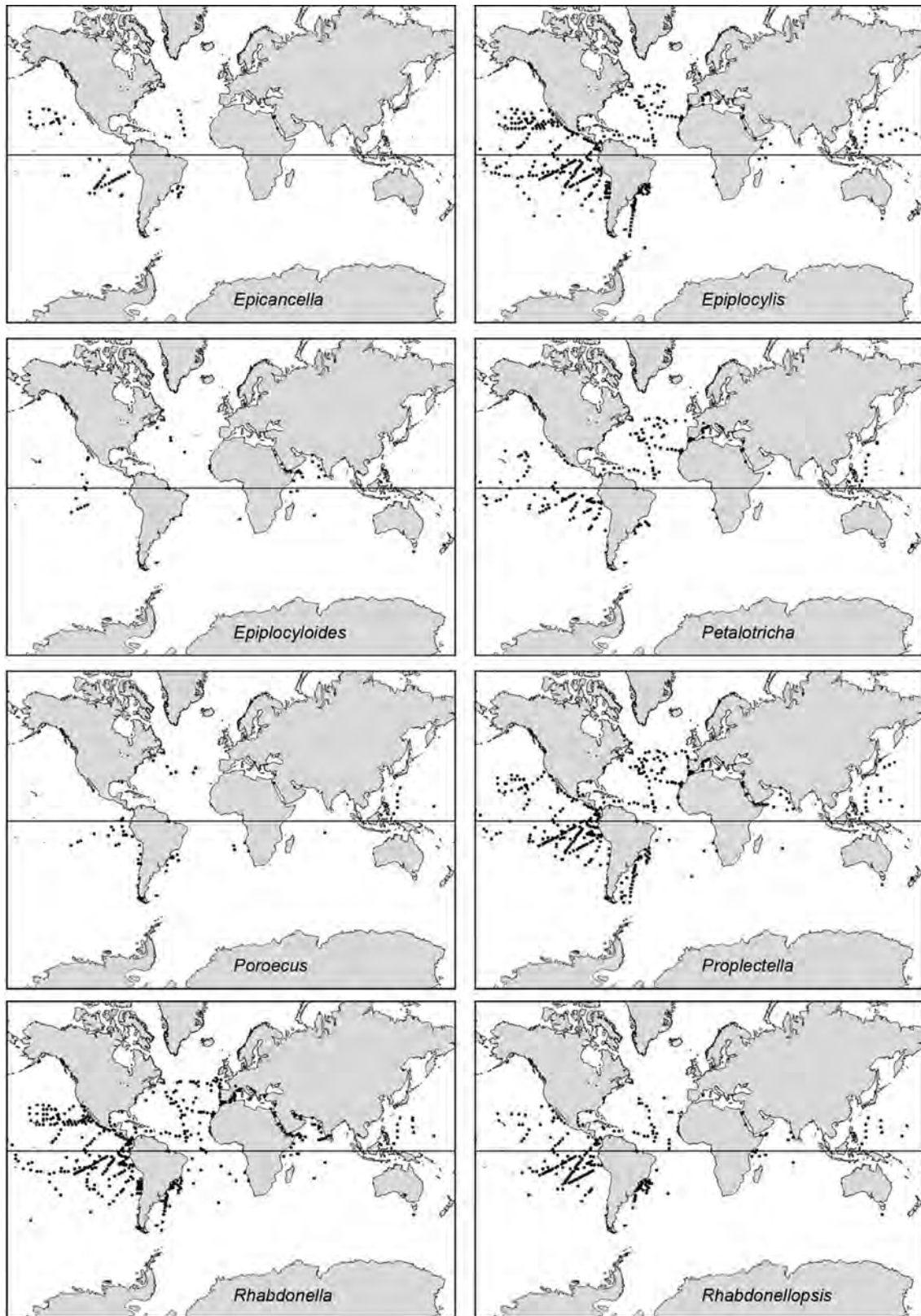
Fig. 10.6 Warm–temperate distributions are shown by *Epicancella*, *Epiplocylis*, *Epiplocycloides*, *Petalotricha*, *Poroecus*, *Proplectella*, *Rhabdonella*, and *Rhabdonellopsis*.

Fig. 10.7 Warm–temperate distributions are shown by *Undella*, *Undellopsis*, *Xystonella*, and *Xystonellopsis*.
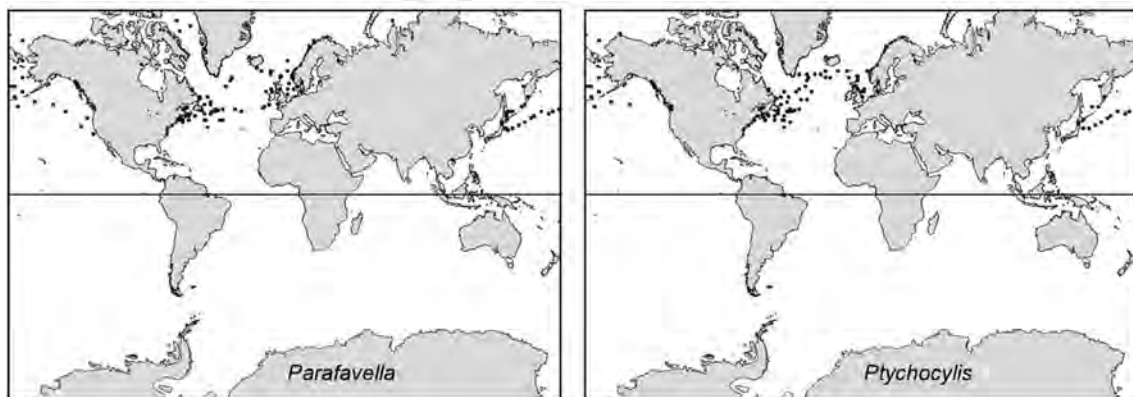
Fig. 10.8 Boreal. Boreal distributions, restricted to the far north but reported from both neritic and open waters, are shown by the genera *Parafavella* and *Ptychocylis*.
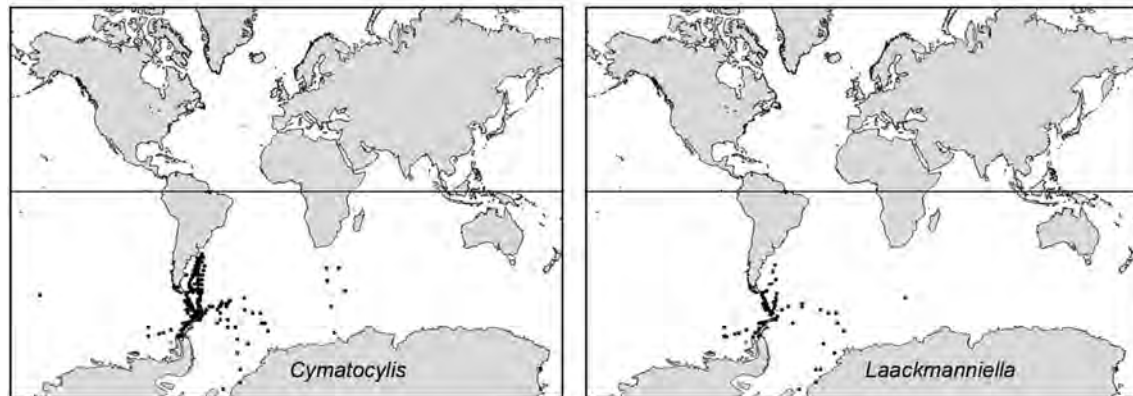
Fig. 10.9 Austral. Austral distributions, restricted to the far south but reported from both neritic and open waters, are shown by the genera *Cymatocylis* and *Laackmanniella*.

everywhere" because protists are effectively not dispersion-limited. The combination of large global population sizes, short generation times, and lack of geographic barriers is thought to prevent endemism among protists (see, for example, Fenchel & Findlay 2004). Indeed many protists form cysts, including tintinnids (see Chapter 7), which can be transported actively by other organisms or passively by water or wind, giving some forms a potentially worldwide distribution. The opposing view is that varying degrees of endemism exist among protists and that few, if any, "species" of protists are truly cosmopolitan (see, for example, Foissner et al. 2009). This view has in recent years become established as the dominant school of thought (see, for example, Fontaneto & Brodie 2011).

In examining the biogeographic patterns of tintinnids, there are some tintinnid "specificities" worth recalling. Many investigations have relied on the same taxonomic references (i.e., Kofoid & Campbell 1929, 1939) regardless of the area under study. This is understandable as region-specific works are often non-existent. However, reliance on the same references, combined with a natural tendency to assign taxa established names, likely increases the chance that species found will be a subset of those illustrated in Kofoid & Campbell (1929). Thus, the distributions of some species may be artificially expanded.

The fact that lorica morphology is the basis of tintinnid identification, and lorica morphology can be variable, also complicates biogeographic studies. For example, tintinnids of diverse genera (*Favella*, *Epiplocylis*, *Xystonella*) can produce an alternative, "coxlielliform" lorica, which was only recognized as an abberant lorica form in the 1970s (Laval-Peuto 1977, 1981). Some lorica characteristics, typically length, can be quite variable. One morphometric study of the genus *Cymatocylis* (Williams et al. 1994) found that 45 lorica morphologies described as separate species could only be reliably sorted into five distinct morphotypes. Often, species identifications are made based on one or a few loricae, which may not be typical forms. Lorica-based species identifications are not always unambiguous. Partly for this reason, the distributions presented here are largely for genera.

A third consideration is the possibility of relatively recent changes in distribution due to phenomena such as climate change, ecosystem changes, construction of canals, or transport of tintinnids through ballast water (Pierce et al. 1997). This is very difficult to assess as many areas have not been well sampled and the lack of a report of a species cannot be taken as proof that the species was not already present. Range expansion of some species may have occurred, for example into the Black Sea, with major ecosystem shifts (Gavrilova & Dolan 2007).

The "invasive species" among tintinnids have received no attention as tintinnids, unlike dinoflagellates and diatoms, do not form harmful blooms nor are they likely to shift trophic food-web structure as known from certain ctenophores. However, at least one
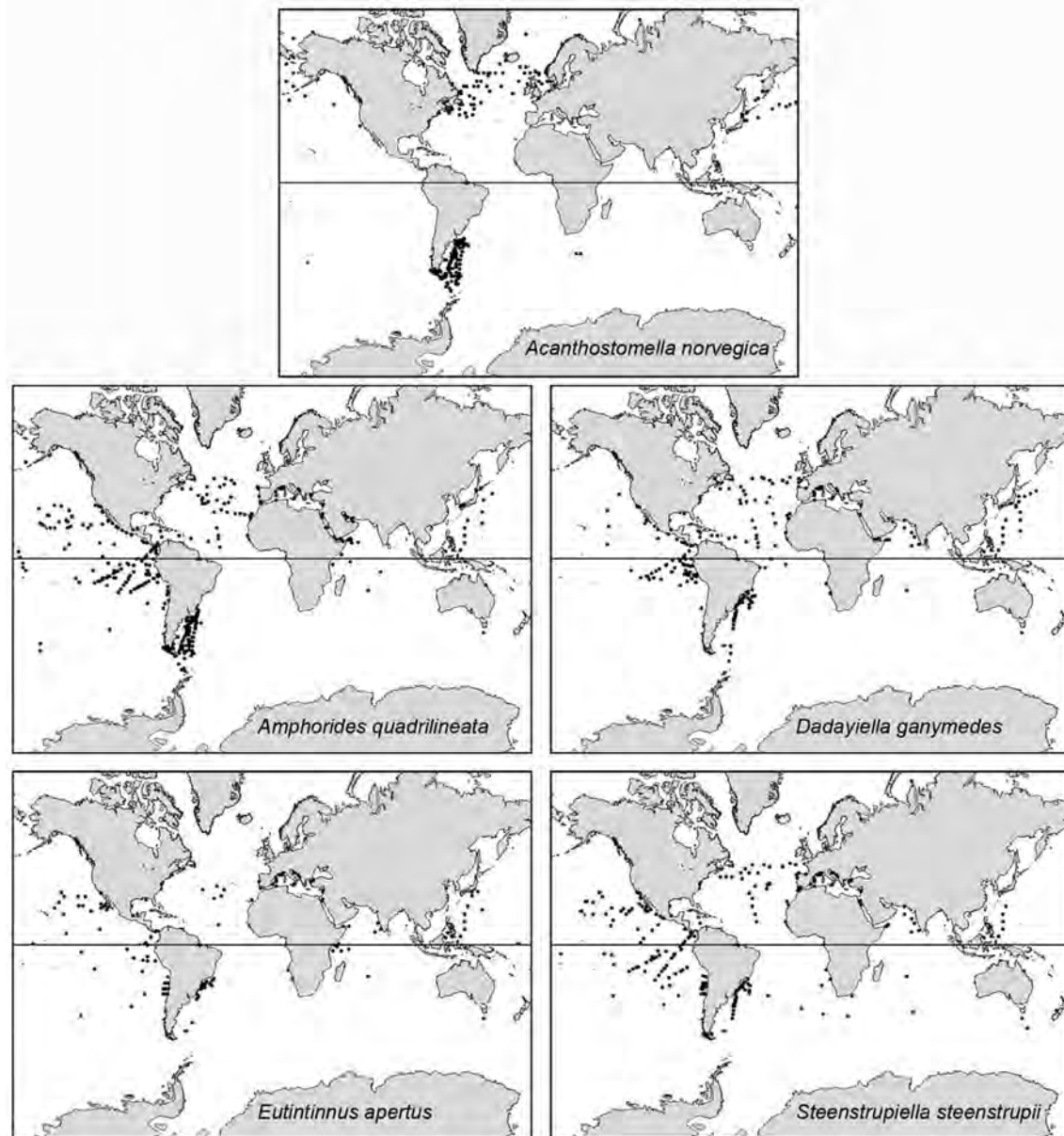
Fig. 10.10 The most common species of the cosmopolitan genera show restricted distributions. *Acanthostomella norvegica* is absent from warm waters. The four most commonly reported and widely distributed tintinnid species (*Amphorides quadrilineata*, *Dadayiella ganymedes*, *Eutintinnus apertus*, *Steenstrupiella steenstrupii*) are absent from far northern and southern seas.
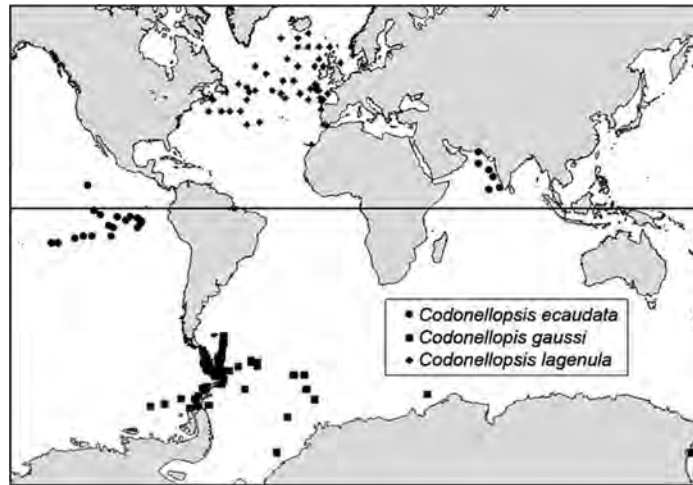
Fig. 10.11 Some frequently reported species show endemic distributions or highly restricted distributions. *Codonellopsis ecaudata* has been reported only from the Indian and central Pacific Oceans. *Codonellopsis gaussi* is found only in the Southern Ocean and *C. lagenula* in the North Atlantic Ocean.

tintinnid species may have expanded its range in recent years, perhaps through transport of ballast water. It is a species most commonly known as *Tintinnopsis corniger*, a large tintinnid with a distinctive, branching, hyaline aboral extension, unmistakable when seen. Such an unusual *Tintinnopsis*, with a large hyaline branching aboral horn, was first mentioned by Busch in 1925 and described as a form of *T. karajensis* from the Strait of Makassar in Indonesia. A very similar tintinnid, from Peter the Great Bay in the northern, sub-polar sector of the Sea of Japan, was described as *Rhizodomus tagatzi* by Strelkow and Wirketis in 1950 without reference to Busch (1925). The Strelkow and Wirketis description, though, was in a Russian-language publication, so that when Hada (1964) found the species in Hiroshima Bay in the Inland Sea of Japan, he described it as a new species, *Tintinnopsis corniger*, again with no reference to Busch 1925. It is very unlikely that Hada would have missed the species in his earlier studies of tintinnids in Japanese waters (Hada 1932a, b, c, 1937). It is now routinely reported from Japanese waters (Nakashima & Kimoto 1987; Nomura et al. 1992; Kamiyama 1994a; Kamiyama & Tsujino 1996; Akizawa et al. 1998; Nakamachi & Iwasaki 1998; Godhantaraman & Uye 2003; Nakane

et al. 2008) and Korean waters (Yoo et al. 1988; Yoo and Kim 1990).

Outside of Asia, *Tintinnopsis corniger* was first reported in the Gulf of Mexico and Caribbean Sea (Balech 1968; Lubel 1974) then in the Arabian Gulf (Sharaf 1995). Later the species was found in coastal waters of the western Mediterranean Sea where it was once again described as a new species, *Tintinnopsis nudicauda* (Paulmier 1997) without reference to Busch (1925), Strelkow & Wirketis (1950), or Hada (1964). It was found in the North Sea in Dutch coastal waters in 2004 (Verweij et al. 2005). In recent years, *T. corniger* has been reported from Mission Bay, California (Elliott & Kaufmann 2007). In the Mediterranean it has been found in a saline lake near the Straits of Messina in the Central Mediterranean (Sacca et al. 2008), in the Eastern Mediterranean in Lebanese coastal waters (Abbou-Abi Saab 2008), Damietta Harbor, Egypt (Dorgham et al. 2009), and most recently in the Sea of Marma (Durmas et al. 2011) and the Black Sea (Gavrilova 2010). Tintinnids have been found in the ballast water of cargo ships (Pierce et al. 1997, Chandrasekera & Fernando 2009), including *T. corniger* (David et al. 2007). The far-flung and disjunct distribution (Fig. 10.12) is very suggestive of trans-
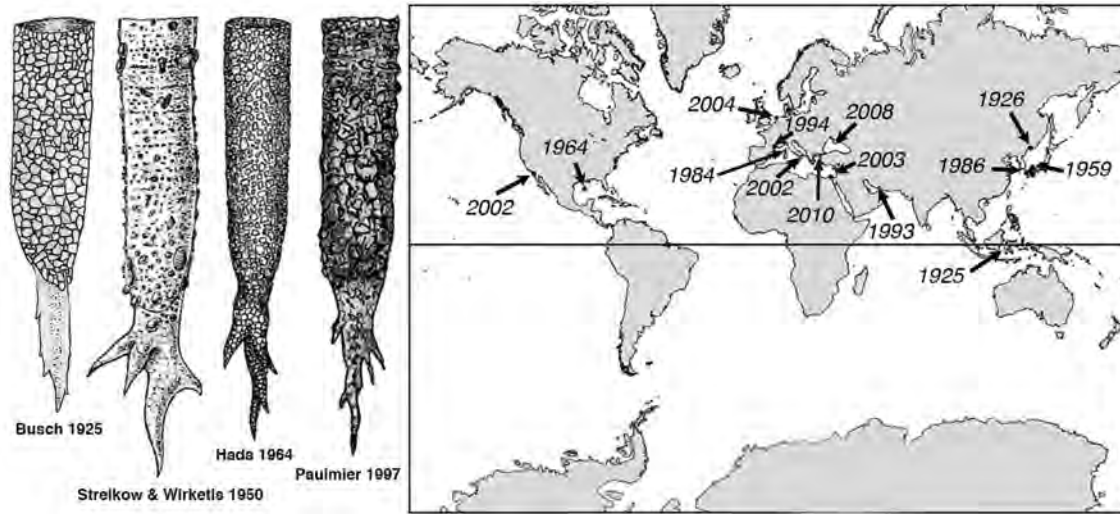
Fig. 10.12 *Tintinnopsis corniger* is a large, distinctive species which apparently has been described four times and reported from widely scattered locations suggestive of ballast-water transport or other artificial means of distribution. The left panel shows illustrations from published descriptions. The right panel shows locations from which the species has been reported; the years refer to when samples were collected: 1925 = Busch (1925), 1926 = Strelkow and Wirketis (1950), 1959 = Hada (1964), 1964 = Balech (1968), 1984 = Paulmier (1997), 1994 = Lam Hoai et al. (1997), 2002 Mediterranean = Saccà et al. 2008), 2002 N. America = Elliot et al. (2007), 2003 = Dorgham et al. (2009), 2004 = Verweij et al. (2005), 2008 = Gavrilova (2010), 2010 = Dormus (2011). We use *T. corniger* as it is the common name in the literature. Saccà et al. (2012) have re-described the species as *Rhizodomus tagatzi*.

port by ballast water (all the locations are near major shipping channels) or other human activities.

Distribution–abundance relationships

The global biogeography of tintinnid taxa clearly indicates a large heterogeneity in distributions. There are a few very widespread taxa, whereas most appear to have a "patchy" distribution, whether they be neritic or open-water forms. Do these differences reflect any quantitative differences? A correlation of average abundance and spatial distribution is a very common phenomenon when comparing ecologically and phylogenetically related taxa (see, for example, Brown 1984). The positive relationship between abundance and distribution is a fundamental ecological pattern, the precise nature of which appears to be variable, perhaps related to the scales considered (see, for

example, Holt et al. 2002; Blackburn et al. 2006) and many mechanisms have been proposed to account for the pattern (Borregaard & Rahbek 2010). The interested reader is directed to the reviews by Blackburn et al. (2006), Borregaard & Rahbek (2010), and Gaston & He (2011) for detailed considerations of the relationship. Here we will be concerned only with the deceptively simple question: are widespread tintinnids found in higher concentrations compared with forms with apparently restricted or patchy distributions?

The interest in examining this question is twofold. First, it is to establish if indeed tintinnids conform to the general pattern of abundant species being more widespread than rare or less-abundant species. The relationship has not been examined for organisms of the marine plankton. Among terrestrial organisms, exceptions to the general distribution–abundance rule have been found among taxa with great dispersal capacity, specifically some groups of birds (Symonds &

Johnson 2006) and butterflies (Paivinen et al. 2005). Second, if distribution does not reflect abundance, then restricted or patchy distributions could be artifacts of inadequate sampling effort.

Answering the simple question of the relationship between distribution and abundance requires detailed data from studies on large geographic scales, which are rarely reported. However, the few data available clearly show a positive relationship between spatial distribution and average abundance among tintinnid species (Fig. 10.13). The data are from different systems sampled on distinct geographic scales: the tropical Southeast Pacific Ocean, 22 stations along a cruise track of 8000 km (Dolan et al. 2007), and the Sub-

Polar Straits of Magellan, 18 stations along a 500 km cruise track (Fonda Umani et al. 2011). In both data sets, "distribution", as the number of stations from which a species was recorded, was positively related to the overall average abundance of the species. Similarly, the distribution of a tintinnid species relative to other species, its "rank distribution", was correlated with the overall abundance rank of the species. Thus, spatial distribution does appear to be positively related to abundance in tintinnids.

Another component of distribution–abundance relationships is temporal rather than spatial occurrence. The question then becomes, "are temporally persistent tintinnids found in higher concentrations
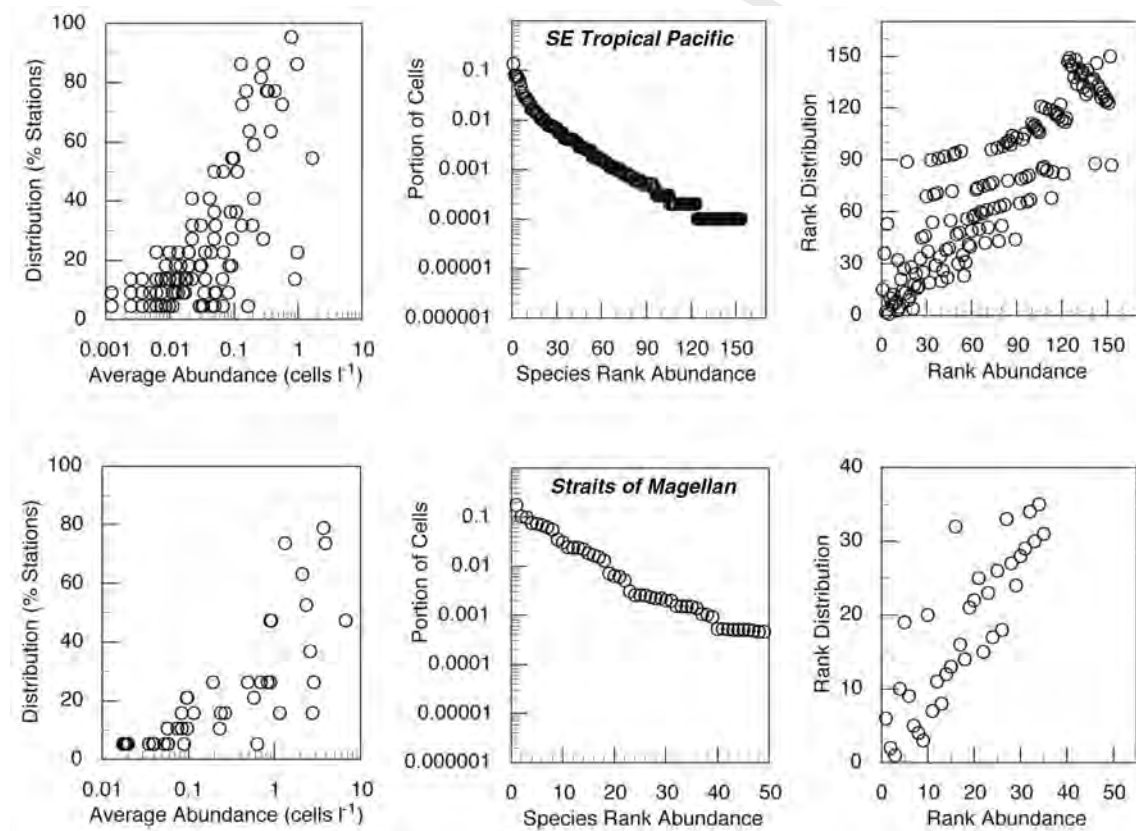
Fig. 10.13 The common pattern of a positive relationship between abundance and the extent of spatial distribution is shown by tintinnid species. Data from the southeast tropical Pacific Ocean are from 22 stations sampled in 2004 along a cruise track of about 8000 km between the Marquise Islands and the coast of Chile (Dolan et al. 2007). The Straits of Magellan data are from 18 stations sampled in 1991 along a 500 km cruise track (Fonda Umani et al. 2011). For both data sets, average abundance represents abundance averaged over all the stations sampled and species rank abundance for a pooled data set.
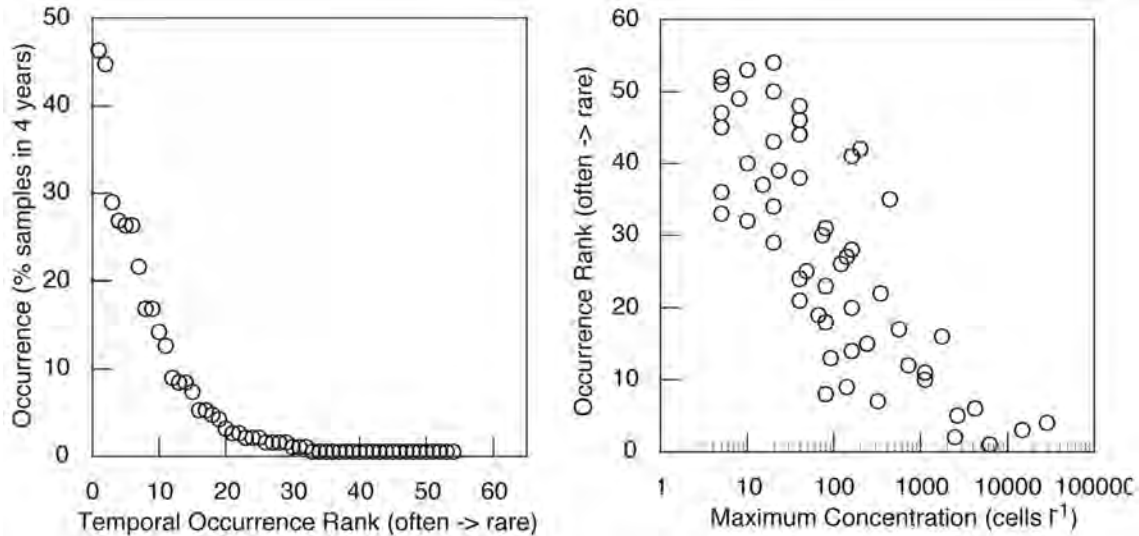
Fig. 10.14 Tintinnid species that are the most often present in a time-series are also those species that reach the highest abundances. Data from weekly sampling of the Gulf of Naples (Italy) over 4 years (Modigh & Castalado 2002).

compared with forms with apparently ephemeral distributions?" The answer requires time-series data. Perhaps the most complete of these is for a coastal system, the Gulf of Naples, which was sampled weekly for 4 years (Modigh & Castalado 2002). The most perennial species was present in less than half the weekly samples, indicative of seasonal changes in the species composition of the tintinnid assemblage (Fig. 10.14). Nonetheless, maximum abundance of a given species was positively related to its frequency of occurrence.

Overall, tintinnids that are widely distributed spatially are also the most abundant forms. However, it should be noted that global patterns are not the same as local patterns. The most widespread species globally are not necessarily the most common within a given system. For example, the most widespread and abundant species in the Straits of Magellan in the 1991 cruise was *Acanthostomella norvegica*, which is restricted to polar and sub-polar waters. Likewise, the species found most often in the Naples time-series was *Tintinnopsis beroidea*, a species found in coastal waters.

Latitudinal diversity gradient

Common to many groups of organisms, both terrestrial and marine, is the distinct increase in species diversity from high to low latitudes. This pattern, the latitudinal diversity gradient, is perhaps the most familiar and studied of all phenomena in biodiversity. The gradient has been described as "remarkable for its pervasiveness, its lack of a generally agreed explanation, and for the plethora of explanations put forward" (Williamson 1997). One author has gone so far as to title a chapter in a book on diversity "The holy grail of ecology: latitudinal gradients" (Adams 2009). Observations of the marked diversity of pelagic tropical fauna and flora compared with the temperate zone go back to the 19th century (see, for example, Haeckel 1893). For tintinnids, Kofoid remarked that a sample from tropical waters will contain few individuals but lots of species compared with a sample from polar waters with lots of individuals of very few species (Kofoid 1930). Nonetheless, not long ago the existence of latitudinal diversity gradients in the sea was questioned (Clarke 1992). Now it is recognized that many marine organisms, if not most groups, do exhibit the gradient. A latitudinal diversity gradient characterizes marine organisms ranging from fish and macroplankton (Angel 1997) to benthic invertebrates (Macpherson 2002), bacteria (Fuhrman et al. 2008), and perhaps even viruses (Angly et al. 2006). The details of the marine gradients have been reviewed by Hillebrand (2004) and the relative importance of the
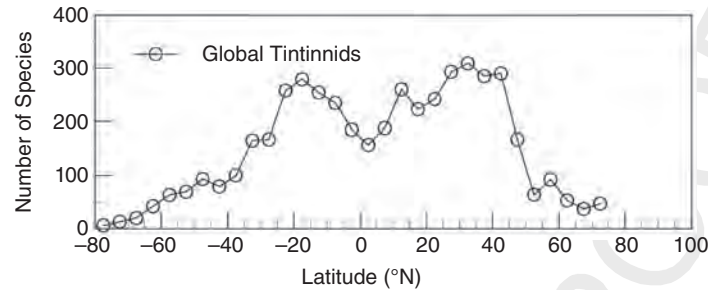
Fig. 10.15 Tintinnids show a typical latitudinal diversity gradient. Total species richness in bands of 5° of latitude from the database of the species records in Pierce & Turner (1993) updated for this chapter.

different mechanisms responsible remains an active area of debate (see, for example, Buzas et al. 2002; Allen & Gillooly 2006; Corliss et al. 2009; Schemske et al. 2009). Here the discussion will be limited to the general pattern shown by tintinnids as it compares with those known from other planktonic groups, along with the mechanisms proposed to explain latitudinal diversity gradients in the plankton.

The tintinnid pattern described here is based on records of morphologically defined taxa, as are virtually all the known latitudinal gradients. However, it should be mentioned that distributions of morphologically defined taxa may not completely correspond with patterns of genetically defined taxa. Cryptic species are known from a large range of planktonic groups: foraminifera (de Vargas et al. 1999), nanoflagellates (Slapeta et al. 2006), diatoms (Kooistra et al. 2008), dinoflagellates (Darling et al. 2004), and copepods (Goetz & Ohman 2010). As previously mentioned among tintinnids, cryptic species, genetically distinct groups of morphologically identical organisms, are not known. Plastic species, those that display very different morphologies and have been described as distinct taxa, are known from studies of lorica development in *Favella* (Laval-Peuto 1977), sequence data in Petalotricha/ Cyttarocylis (Bachy et al. 2012) and are suspected from morphometric studies of *Cymatocylis* (Williams et al. 1994). How diversity patterns might differ between morphologically defined and genetically defined species is, unfortunately, unclear at present.

The stereotypical latitudinal diversity gradient is one of low species richness near the poles, increasing toward the equator with a peak at about 15–20° both north and south, and a slight inflection or decrease around the equator. This "textbook" pattern has been described for tintinnids (Dolan & Gallegos 2001; Dolan

et al. 2006) and is shown in Fig. 10.15, based on the global species records in Pierce & Turner (1993) and updated for this chapter.

Among other planktonic groups, the typical pattern of tintinnids also characterizes copepod diversity (Fig. 10.16). For copepods and another group of zooplankton, the foraminifera, the latitudinal trend in species richness has been statistically linked to annual average sea surface temperature by a positive curvilinear relationship (Rutherford et al. 1999; Woodd-Walker et al. 2002; Rombouts et al. 2009), but somewhat distinct explanations have been proposed for the nature of the mechanism. For Rutherford et al. (1999), average sea surface temperature is a proxy measure of the average depth of the surface mixed layer, thus representing habitat size. According to this explanation, deep surface layers contain more species because they contain more spatial niches. Alternatively, areas of distinct sea surface temperature characterize areas that differ in temporal patterns and variability of primary production and thus represent areas of different habitat stability or seasonality (Woodd-Walker et al. 2002; Rombouts et al. 2009). The areas of marked variability in water column structure and primary production are lower in species richness, presumably because such systems are poorer in the number of distinct, stable, niches owing to temporal variability of the environment. It should be noted that the explanations of habitat size versus stability are not mutually exclusive. Although the commonality of patterns among tintinnids, copepods, and foraminifera suggests a single "zooplankton" gradient, the same cannot be said for phytoplankton.

Based on the few reports that exist, phytoplankton show distinct group-specific and ocean-basin-specific patterns. Different patterns for diatoms and coccolitho-
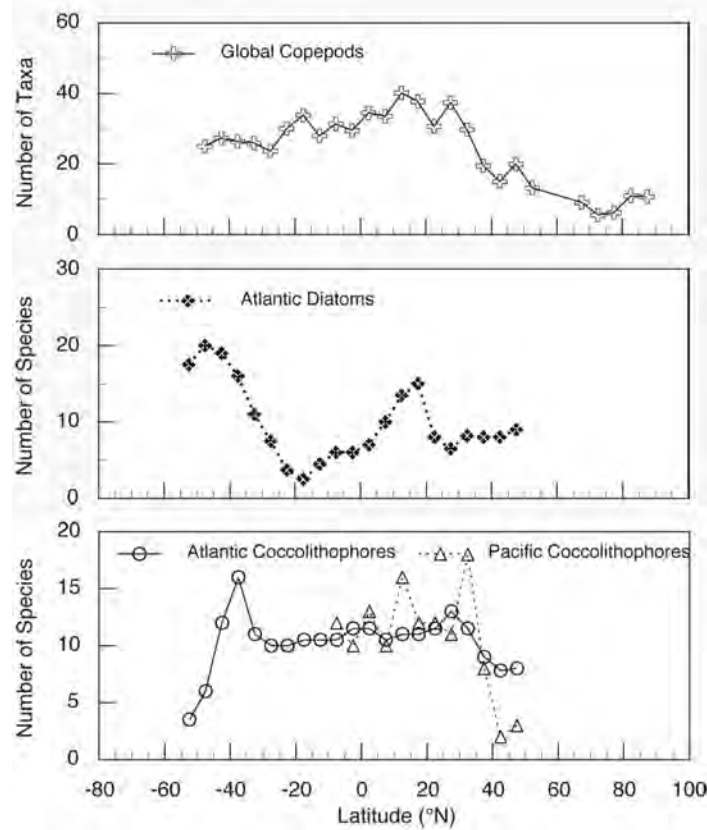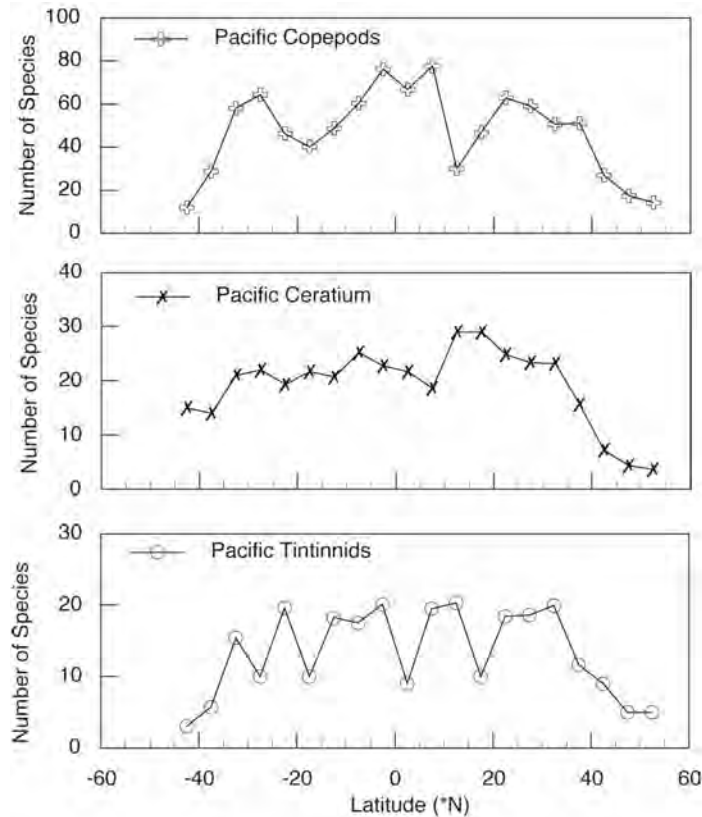
Fig. 10.16 Latitudinal diversity gradients of different groups of planktonic organisms can be similar to tintinnids, such as copepods, whereas those of diatoms and coccolithophores appear distinct. The copepod data were taken from figure 2a in Rombouts et al. (2009) and averaged in bands of 5° of latitude. The y-axis is labeled "taxa" as some species were grouped by genus. The Atlantic diatom and coccolithophore data were taken from figure 1c in Cermano et al. (2008). The Pacific coccolithophore data were taken from figure 6 in Honjo & Okada (1974), surface layer, and averaged in bands of 5° of latitude.

phores have been described for the Atlantic Ocean (Cermano et al. 2008). Diatom diversity appears to be highest in high latitudes and areas of upwelling, and is lower in tropical latitudes, suggesting a positive relationship with mixed water columns and high nutrient conditions (thus opposite from that of tintinnids and other zooplankton). Coccolithophore diversity, while sharing the same peaks with diatoms in nutrient-rich zones, remains relatively high throughout the Central Atlantic. The distinct patterns were explained as reflecting diatom adaptation to high-energy, high-nutrient conditions, and coccolithophores as adapted to low-energy, low nutrient conditions. Coccolitho-

phore diversity in the Central and Northern Pacific Ocean was also described by Honjo & Okada (1974). The same basic pattern as that described for the Atlantic is evident with a relatively high diversity across the Central Pacific Ocean although the North Pacific appears to be species-poor relative to the North Atlantic Ocean (Fig. 10.16).

In reality, it is somewhat unclear whether or not tintinnids are actually similar to, or differ from, other groups in large-scale patterns of diversity because descriptions are invariably based on analysis of distinct data sets, derived from sampling on different time or space scales, potentially confounding patterns.

Fig. 10.17 Latitudinal diversity gradient in the Pacific Ocean of copepods, *Ceratium* species, and tintintinids are similar. Based on data from Cruise VII of the Carnegie (Campbell 1942; Wilson 1942; Graham & Bronikovsky 1944). Species richness was averaged in bands of 5° of latitude.

However, data from the Cruise VII of the Carnegie in 1928–1929 represent an exception as different groups of the zooplankton and phytoplankton (tintinnids, copepods, and species of the dinoflagellate genus *Ceratium*), were catalogued from the same surface layer samples, allowing direct comparison of species abundance patterns. The complete data on the three groups suggest similar global latitudinal diversity gradients (Dolan 2011). Here the patterns of the Pacific Ocean based on the Carnegie reports (Campbell 1942; Graham & Bronikovsky 1944; Wilson 1942) will be considered because data on the Pacific populations are often sparse (see, for example, Rutherford et al. 1999; Rombouts et al. 2009) and the Carnegie data are dominated by Pacific Ocean stations (126 of the 160 stations).

A very similar latitudinal gradient of the Pacific Ocean populations of tintinnids, copepods, and *Ceratium* is evident but is relatively irregular for tintinnids compared with copepods and *Ceratium* (Fig. 10.17). The patterns for Pacific Ocean tintinnids, copepods, and *Ceratium* all resemble closely that of the "global" pattern for zooplankton in which diversity is thought to be inversely related to variability in primary production and/or positively related to average surface layer depth. Thus, resource stability and/or habitat size are associated with high diversity. Notable is the fact that *Ceratium* in the phytoplankton shares the pattern as tintinnids and copepods. *Ceratium* may not be typical of the phytoplankton. Some species of *Ceratium* are known to be mixotrophic, although mixotrophy appears to be a relatively minor nutritional mode
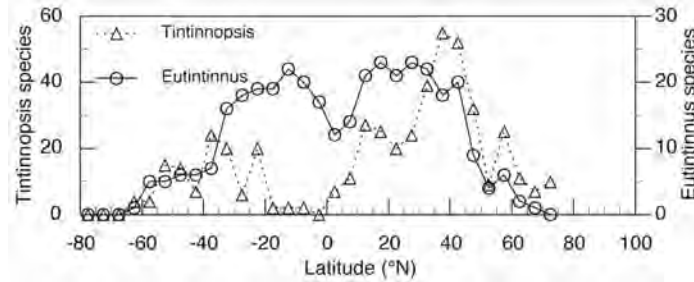
Fig. 10.18 Latitudinal diversity gradients of the genera *Tintinnopsis* and *Eutintinnus* are distinct, reflecting adaptation to different types of system. Total species richness in bands of 5° of latitude are from the database of the species records in Pierce & Turner (1993) updated for this chapter.

(Bockstahler & Coats 1993). There may be no general pattern characteristic for different phytoplankton taxa. It appears in comparing diversity trends of Atlantic Ocean diatoms and coccolithophores that individual groups of phytoplankters differ considerably in their large-scale diversity patterns.

Just as different major phytoplankton taxa show distinct large-scale patterns of diversity, patterns of specific groups within a given taxon can be distinct as a lower level taxon can be adapted to, or characteristic of, a particular type of environment. This is easily seen in tintinnids by comparing two species-rich genera: *Tintinnopsis* and *Eutintinnus*. *Tintinnopsis* species, with their loricae agglutinated with small mineral particles, are essentially restricted to neritic shallow waters and usually dominate tintinnid assemblages in bays and estuaries, especially those in temperate climates. *Eutintinnus* species, although found among neritic assemblages, are very commonly found in open waters from temperate to tropical zones and are often the dominant form in tropical assemblages. The two genera display very different biogeographies (Fig. 10.4) and show very different latitudinal diversity gradients (Fig. 10.18). *Tintinnopsis* species richness is very low in the tropics and peaks in the temperate zones of both the southern and the northern hemispheres at about 40°. In contrast, *Eutintinnus* species richness resembles the general global tintinnid pattern, being highest in the tropics and sub-tropical areas.

Among other zooplankton, the same phenomenon of distinct differences in biogeographic patterns among particular taxa is also known. For example, different patterns characterize calanoid and cyclopoid copepods in the estuaries of eastern North America. Species richness is highest in temperate systems for calanoid copepods whereas cyclopoid copepods are more species-rich in sub-tropical estuaries. The differences were explained as likely reflecting calanoid copepod adaptation to the large seasonal changes typical of temperate systems (Turner 1981).

Tintinnids, as a whole, show a latitudinal diversity gradient similar to that of copepods and *Ceratium*. It is reasonable to expect that the same mechanism explains the pattern in all three groups and that it can be linked directly or indirectly with sea surface temperature, as shown for copepods and foraminfera (Rutherford et al. 1999; Woodd-Walker et al. 2002; Rombouts et al. 2009). However, the precise nature of the mechanism (e.g., exactly how environmental stability promotes diversity or conversely how environmental variability inhibits diversity), remains to be identified.

10.3   ASSEMBLAGES OF COASTAL SYSTEMS

Seasonal changes in species richness

Very early in the 20th century, under the influence of a need to understand fisheries dynamics, studies of plankton shifted focus from taxonomy to community and population biology, with particular attention devoted to annual plankton cycles (Mills 1989). Temporal variability of planktonic organisms in coastal systems was already well known; Karl Brandt (1901) remarked, "To know the plankton of a body of water, it is necessary to repeat sampling at the shortest interval of time possible over at least a year". It was soon

recognized that seasonal changes in species compositions were not due to shifts in the locations of waters masses containing different assemblages but rather the waxing and waning of different species within the system. Some of the earliest studies on seasonal changes in planktonic populations concerned or included tintintinnids (see, for example, Laackmann 1908; Lohmann 1908; Lebour 1917). Given the long history of European studies, it is perhaps not surprising that although tintinnid assemblages have been studied in a very wide range of coastal systems, Mediterranean and North Atlantic systems have received the greatest attention (Table 10.2).

Reports from nearly every system describe very distinct seasonal changes in the occurrences of individual species and species richness. Perhaps the most intensive time-series available, the Gulf of Naples sampled weekly for 4 years, showed that none of the 10 most common species were found even half the time and most less than a third of the time (Fig. 10.14). Differences in the assemblages and patterns in different systems have led to the suggestion that these constitute distinct "tintinnid community fingerprints" for each system (Modigh & Castalado 2002). Although no two systems appear identical in detail, quite similar qualitative patterns have been reported from disparate systems.

An apparently common pattern is that species with hyaline loricae constitute the bulk of the community in the summer months whereas species with agglutinated loricae dominate in winter. Thus, the summer communities of the tropical São Sebastião Channel in Brazil and a Mangrove system in southeast India are dominated by species with hyaline loricae (*Eutintinnis*, *Dadayiella*, *Amphopellopsis*) and the winter assemblage by species with agglutinated loricae (*Tintinnopsis*, *Stenosemella*, *Codonellopsis*). Such a pattern, first reported for the Kiel Bight (Laackmann 1908), has been reported for a surprising variety of coastal systems: the Bay of Fundy (Middlebrook et al. 1987), Narragansett Bay (Verity 1987), Mission Bay in Southern California (Elliott & Kaufman 2007), the Gulf of Naples (Modigh & Castalado 2002), and Hiroshima Bay (Kamiyama & Tsujino 1996). The pattern appears to extend from the Arctic waters of the White Sea, where *Helicostomella* dominates in mid-summer (Burkovsky 1976), to Antarctic sub-polar waters, where the springtime community in the Straits of Magellan was dominated by *Tintinnopsis* spp. and the autumn assemblage by *Acanthostomella* (Fonda Umani et al. 2011).

Exceptions to the general pattern of a seasonal shift from species with hyaline loricae to those with aggultinated loricae have been reported. A nearly invariant, *Tintinnopsis*-dominated assemblage characterized the Bahia Blanca Estuary in Argentina. In waters near the Isle of Man in the northern Irish Sea, the tintinnid assemblage is dominated year-round by species of *Stenosemella* or *Tintinnopsis* (Graziano 1989). Species with hyaline loricae, which appear in other coastal systems of the North Atlantic in the summer months, were virtually absent. Species with agglutinated loricae may be better adapted to turbulent conditions, which generally correspond with the winter season. The small mineral particles required to build their loricae may not be present in sufficient concentrations in the water column during the summer months in most coastal systems. The year-round dominance of species with agglutinated loricae may then be because some systems are also high-energy, turbulent systems year-round.

Another characteristic common to many different coastal systems is that the transitional periods between winter and summer correspond to the period when species richness is highest (Fig. 10.19). These periods are characterized by assemblages containing species both with hyaline and agglutinate loricae. In contrast to the commonality of such transitional periods representing peak species richness, the period of minimum species richness varies in different regions. In the temperate systems of the Atlantic, the winter months correspond with periods of low species richness, whereas in Mediterranean systems the summer months are the most species-poor.

A variety of temporal patterns in species richness has been reported from tropical and sub-tropical systems, some related to occurrence of the rainy or dry periods. In the mangrove system of southeast India, peak abundances during dry months correspond with peak species richness and abundance (Godhantaraman 2002). In New Caledonia, species richness was strongly correlated with tintinnid abundance (Dolan et al. 2006). These relationships suggest that species richness may be related to overall tintinnid abundance. Comparing numbers of species found and concentrations of tintinnids in some of the seasonal studies (those in which the data could be easily extracted) shows a positive, albeit weak, relationship across different coastal systems (Fig. 10.20).

A general positive relationship between tintinnid total abundance and species richness suggests conditions that allow the development of a dense population

Table 10.2 Studies of seasonal changes in tintinnid assemblages of coastal systems.

| System	Location	Reference
Mediterranean Region		
Black Sea	Romanian coast	Petran 1958
Black Sea	Crimean coast	Dogopolskaya 1940
Damietta Harbor	Egypt	Dorgham et al. 2009
Jounieh Bay	Lebanon	Abboud-Abi Saab 1989
Palm Island	Lebanon	Abboud-Abi Saab 2002
Bozcaada Island	Aegean Sea	Balkis & Wasik 2005
Bay of Buyucekmece Bay	Marmara Sea	Balkis 2004
Mali Ston Bay	Eastern Adriatic	Krsinic 1980
Kastela Bay	Eastern Adriatic	Bojanic 2001
Ionian Sea	Mediterranean Sea	Sitran et al. 2007
Naples	Southern Italy	Modigh & Castaldo 2002
Bay of Villefranche	Southern France	Balech 1959; Rassoulzadegan 1979; Dolan et al. 2006
San Remo	Northeast Italy	Rampi 1948
Gulf of Marseille	Southern France	Balech 1959, Travers & Travers 1971
Thau Lagoon	Southern France	Lam-Hoai et al. 1997
Blanes	Southeast Spain	Margalef 1957
Gulf of Valencia	Southeast Spain	Duran 1951, 1953
Bay of Algers	Algeria	Vitello 1964
North Atlantic		
Bay of Fundy	New Brunswick, Canada	Middlebrook et al. 1987
Bedford Basin	Nova Scotia, Canada	Paranjape 1987a
Long Island Sound	New York, USA	Capriulo & Carpenter 1983
New York Bight	New York, USA	Gold & Morales 1975
Narrangansett Bay	Rhode Island, USA	Hargraves 1981; Verity 1987
Buzzards Bay	Massachusetts, USA	Pierce & Turner 1994
Damariscotta Estuary	Michcigan, USA	Sanders 1987
Gullmar Fjord	Western Sweden	Hedin 1974
Kiel Bight	Baltic, Germany	Laackmann 1908
Isle of Man	North Sea	Graziano 1989
Southampton Water	UK	Leakey et al. 1993
Bay of Cascais	Portugal	Silva 1950
Obidos Lagoon	Portugal	Silva 1953
Nervion Estuary	Northeast Spain	Urrutxurtu 2004
South Atlantic		
São Sebastião	São Paulo, Brazil	Eskinazi-Sant'anna & Bjornberg 2006
Bahia Blance Estuary	Argentina	Barria de Cao 1992
Mauritania and Senegal	West Africa	Duran 1965
Others		
White Sea	Arctic	Burkovsky 1976
Signy Island	Antarctica	Leakey et al. 1994
Hiroshima Bay	Japan	Kamiyama & Tsujino 1996
Akkeshi Bay	Japan	Taguchi 1976
Tokyo Bay	Japan	Nomura et al. 1992
Funka Bay	Japan	Dohi 1982
Gulf of Elat	Red Sea	Kimor & Golandsky 1981
Kuwait	Arabian Gulf	Skryabin & Al-Yamani 2006
Parangipettai	Southeast India	Godhantaraman 2002
Mission Bay	California, USA	Elliott & Kaufman 2007
New Caledonia	South Pacific	Dolan et al. 2006
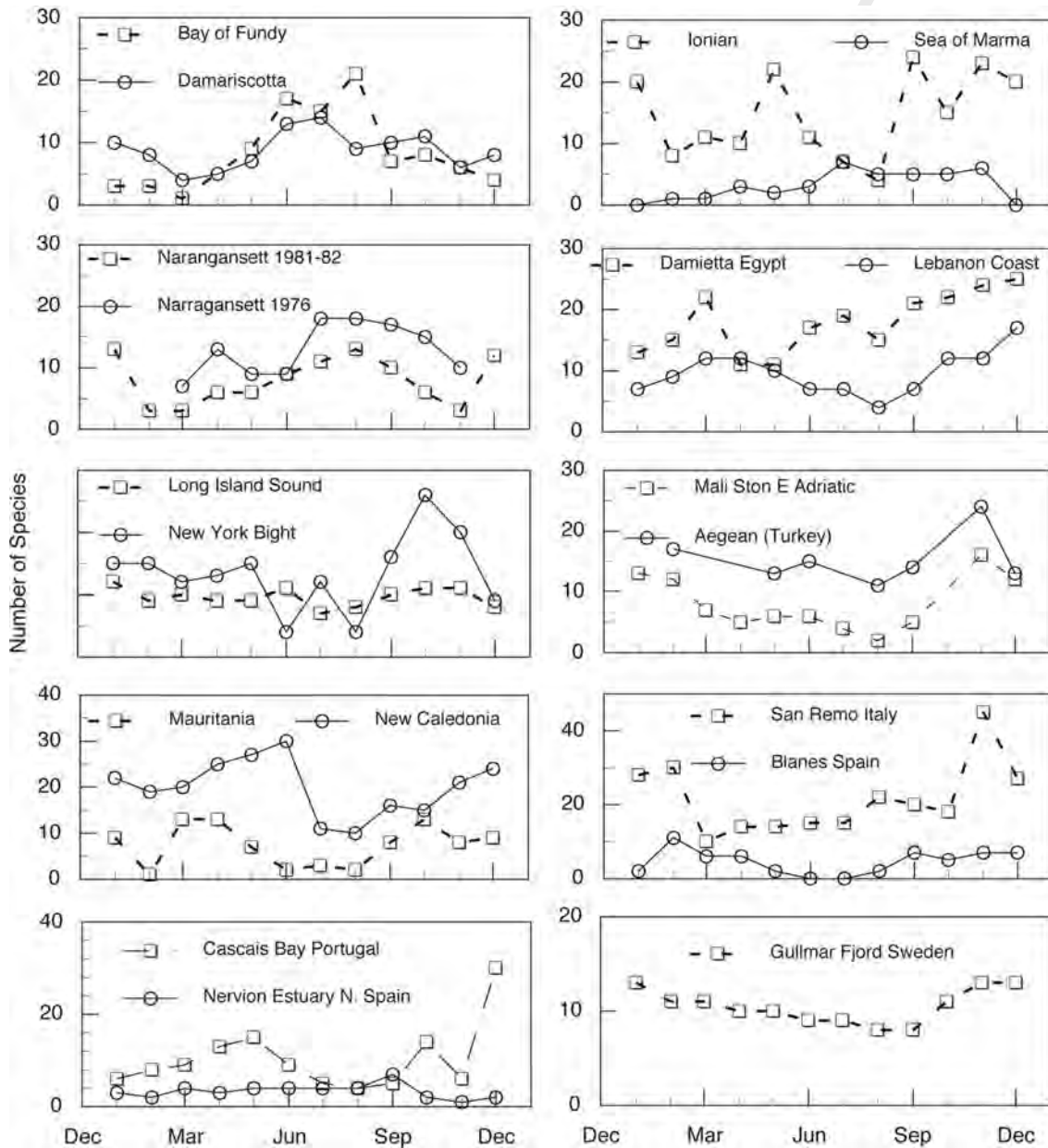
Fig. 10.19 Coastal systems usually show distinct seasonal changes in the species richness of tintinnid assemblages. Data are from sources listed in Table 10.1.
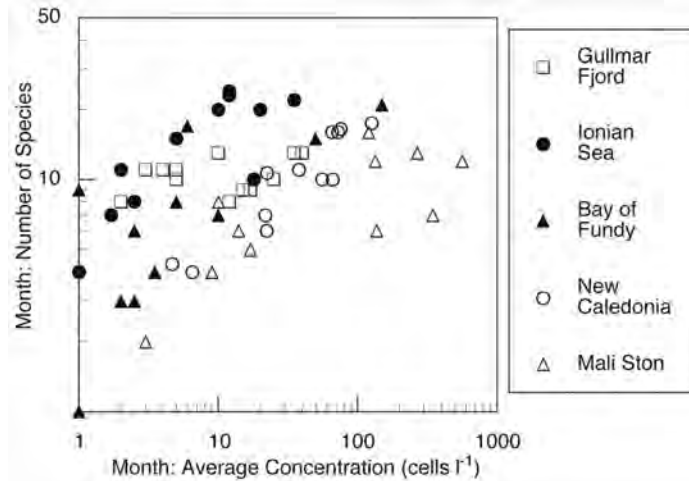
Fig. 10.20 Species richness of tintinnid assemblages in coastal systems is often highest when overall tintinnid concentrations are high. Data are shown by plotting species richness by month against average tintinnid concentration for a wide range of systems. Data sources are references for the systems given in Table 10.2.

of any particular tintinnid species will allow the development of detectable populations of other species. Conversely, conditions that prevent any particular species from becoming abundant are most often poor conditions for all other species as well. The seasons, then, of minimum tintinnid species richness reflect low overall population size corresponding with seasonal minima in primary production, which in temperate systems is in winter and in Mediterranean systems in summer.

Whether the seasonal patterns in coastal systems shown by tintinnids are peculiar to them or are shared with other planktonic groups is unclear. For other planktonic ciliates, owing to the difficulty in precisely identifying ciliates other than tintinnids, there are very few reliable data on seasonal changes in species richness. A perhaps singular exception is the study of Leakey et al. (1993) on the ciliates of Southampton Water, a eutrophic temperate estuary on the southern coast of the United Kingdom in which quantitative protargol staining was used (Montagnes & Lynn 1987) and taxonomic expertise provided by Denis Lynn. Seasonal changes in species richness of ciliates (pooling all taxa) showed the typical tintinnid pattern of North Atlantic coastal systems: that is, a distinct summer peak and winter minimum in species richness. Thus, it would appear reasonable to assume

that temporal trends in species richness are similar for tintinnids and other planktonic ciliates.

There are also some data on seasonal trends of species richness in tintinnids compared with other groups of the "microplankton": diatoms, and dinoflagellates. Many of the earlier reports on seasonal changes in coastal plankton communities focused not on tintinnids but microplankton with, in reality, a primary interest in patterns of diatoms and dinoflagellates. Fortuitously, some of these studies were conducted by investigators with a wide range of taxonomic expertise (i.e., Rampi, Margalef, and Duran), allowing comparison with some confidence of temporal trends in the species richness of tintinnids compared with the other groups of the microplankton.

Seasonal changes in species richness of different groups of the microplankton in three coastal sites of the northwest Mediterranean (San Remo (Italy), Blanes (Spain), and the Gulf of Valencia (Spain)) are shown in Fig. 10.21. The three sites all showed the "Mediterranean" pattern of tintinnid species richness: that is, peaks in spring and autumn with minimum species numbers in winter. Furthermore, all three sites show parallel trends for species richness of diatoms and *Ceratium*. Species richness of all three groups covaried closely in the San Remo and Gulf of Valencia populations. However, diatom and *Ceratium* species
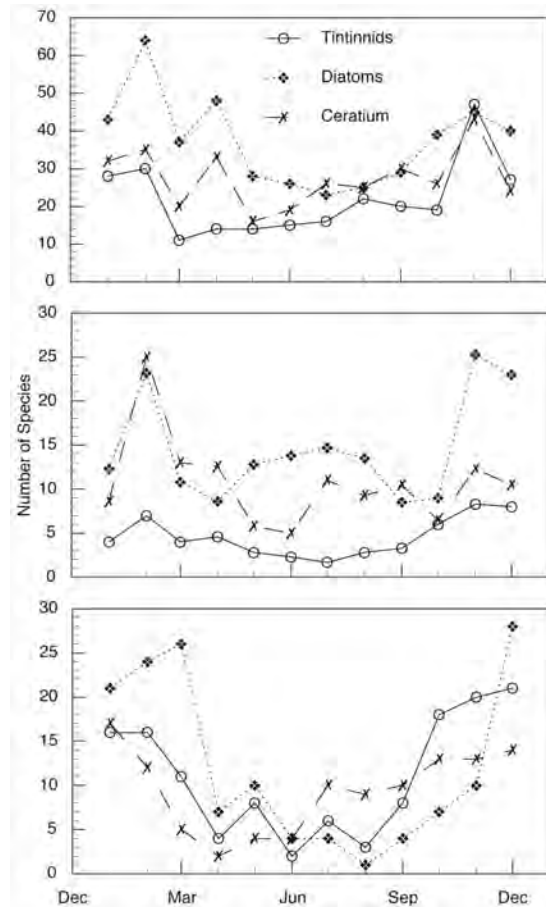
Fig. 10.21 Temporal changes in the species diversity of tintinnids can parallel, or be distinct from, species richness trends in other groups such as diatoms or *Ceratium*. Monthly species richness of tintinnids, diatoms, and *Ceratium* in three coastal systems of the northwest Mediterranean Sea. Top panel, data of Rampi (1948) for San Remo, Italy; middle panel, data (monthly averages) from Margalef (1957) for Blanes, Spain; bottom panel, data from Duran (1953) for the Gulf of Valencia.

richness differed from the tintinnids in the Blanes assemblages. Interestingly, Margalef noted that the seasonal trends of the Blanes populations, with a summer phytoplankton bloom, were unusual for the northwest Mediterranean (Margalef 1957). Nonetheless, it is clear that seasonal changes in the species richness of tintinnids can be distinct from temporal trends in diatoms or *Ceratium* species richness, thus

indicating that different mechanisms govern the diversity of zooplankton and phytoplankton at least in northwest Mediterranean systems.

Seasonal changes in morphotypes

As tintinnid species are distinguished by characteristics of their loricae, changes in species composition of an assemblage corresponds with changes in the loricae of the assemblages. Among the morphological characters of tintinnids, lorica oral diameters have received special attention. For a given species, the oral diameter is a relatively invariant taxonomic characteristic (Gold & Morales 1975, 1976; Laval-Peuto & Brownlee 1986), one that is closely related to both maximum and optimum prey size, among other ecological characteristics (see Chapter 4 and Dolan 2010).

The morphological character "lorica oral diameter" has been used to assess seasonal changes in community characteristics of tintinnid assemblages. It has been examined in different manners, somewhat complicating comparisons. Community average lorica diameter was used to describe assemblages of the Bay of Fundy (Middlebrook et al. 1987), Naragansett Bay (Verity 1987), and Kingston, Jamaica (Gilron et al. 1991). The modal and largest diameters were reported for the Long Island Sound assemblages (Capriulo and Carpenter 1983), median size for assemblages of New Caledonia (Dolan et al. 2006) and the Ionian Sea (Sitran et al. 2007), and the size–frequency distribution of the most abundant species for Funka Bay (Dohi 1982). Nonetheless, all the studies documented changes in the morphotypes constituting the tintinnid community specifically in terms of lorica oral diameters.

An example of a seasonal change in "community average lorica oral diameter" is shown in Fig. 10.22 from Verity's study of Narragansett Bay tintinnids over 3 years (Verity 1987). Verity documented an annual cycle showing a seasonal variability of about 50%, which appears to be typical based on the results of other studies. In Verity's study, community oral diameter was significantly, albeit weakly, related to the portion of chlorophyll-*a* in the size fraction between 10 and 150 μm. Metrics of community oral diameter, whether average, modal, or median, have not been easily and unambiguously related to characteristics of the phytoplankton crop. This is likely because not only phytoplankton resources, but also competition from
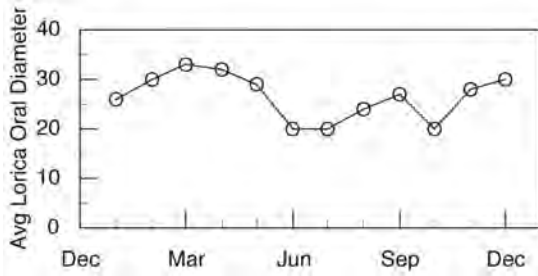
Fig. 10.22 Seasonal change in tintinnid assemblages is reflected in the average lorica oral diameter of the assemblage. The graph shows average monthly values of Narragansett Bay tintinnids from Verity (1987). Changes in community values of lorica oral diameter (average, mode, or median) have been related to changes in phytoplankton size-composition and concentration.

other microplankton grazers as well as species-specific tintinnid mortality from metazoan grazers or parasites, can influence the size of the dominant oral diameter.

Tintinnid assemblages of coastal systems are usually dominated by one species, which more or less defines the community oral diameter. Most other species present will be those with oral diameters distinctly different from that of the dominant species. An example illustrating the distribution of lorica oral diameters in the spring and autumn assemblages of contrasting system, the Gullmar Fjord in Sweden and the Great Lagoon of New Caledonia, is shown in Fig. 10.23. In these assemblages, abundant species are either alone in a size-class of lorica oral diameter or share the size-class with but one other species. In the New Caledonia assemblages, the three most abundant species are in distinct size-classes of lorica oral diameter. It appears to be common that in a given assemblage, the most abundant species are often of distinct oral diameters (compared with the other species present), presumably exploiting prey of distinct sizes (see, for example, Boltovskoy & Alder 1992; Dolan et al. 2009), which is suggestive of resource partitioning among different tintinnid species.

10.4 ASSEMBLAGES OF OPEN WATERS

In contrast to the communities of bays and estuaries, little is known of seasonal changes in tintinnid assemblages in open-water systems. Very few open-water systems have been studied in different seasons and even fewer by the same investigators, assuring a certain comparability among samplings and sample analysis. Detailed quantitative data are completely lacking, with most reports giving little more than brief lists of abundant forms in winter and summer. However, such "occurrence data" do suggest that open-water systems may not exhibit the large seasonal changes in species composition that characterize coastal systems.

For example, the typical seasonal change from a winter assemblage dominated by species with agglutinated loricae to a summer assemblage dominated by hyaline species can be absent. In both winter and summer, the assemblage of the Inland Sea of Japan appears to be dominated by *Tintinnopsis beroidea* and *Stenosemella nivalis* (Godhantaraman & Uye 2001). Likewise, assemblages of "large" tintinnids of the Southern Yellow Sea are dominated by *Stenomella steini*, *Tintinnopsis karajacensis*, and *T. radix* in winter and by *Codonellopsis mobilis* and *T. karajacensis* in the summer. These were both studies of temperate, open, but relatively shallow, waters of the western Pacific Ocean and may be thought exceptional. However, relatively detailed data from a contrasting system, the subtropical Gulf of Mexico, also suggest that seasonal changes in species composition in deep open waters, in which agglutinated species are a minor component, are also slight compared with coastal systems.

The microplankton of the Gulf of Mexico was studied by Balech (1967a, b), who collected samples from a series of 10 cruises in 1964 and 1965 in the Northeast Gulf of Mexico. Of the 10 cruises, four were summer cruises (June–September) and four were winter cruises (December to early March). The pooled summer cruise data represent species lists from 40 stations, and the winter cruise data represent 46 stations, allowing a rough comparison of summer and winter tintinnid assemblages. Furthermore, the occurrences of *Ceratium* species, among other dinoflagellates, were also recorded, allowing a comparison with the species-rich group of phytoplankters known to share temporal patterns of species abundances in the northwest Mediterranean Sea (see, for example, Rampi, 1948; Raybaud et al. 2009).

Balech did not report quantitative data but rather species lists for each of the stations; consequently, occurrence or "occupancy" – describing how widespread or rare was each species – could be estimated simply from the percentage of stations from which a
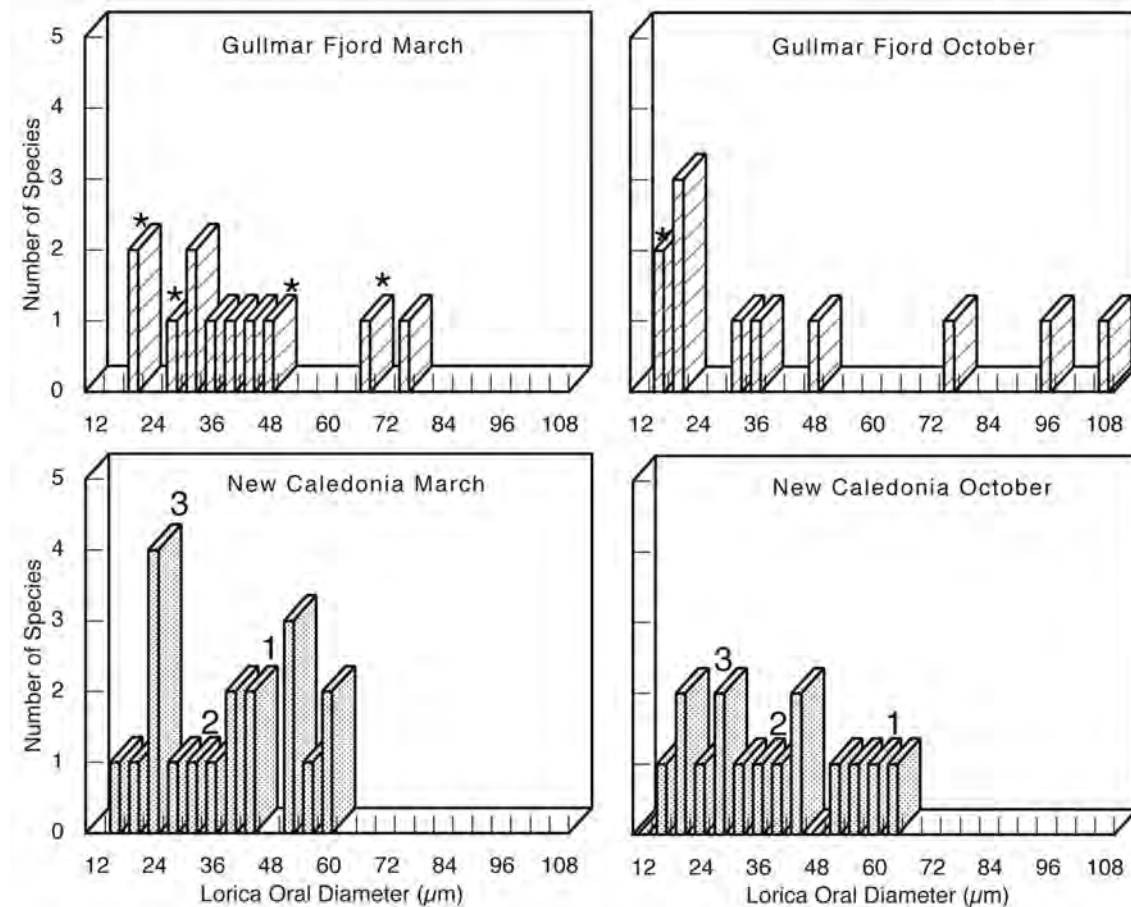
Fig. 10.23 Co-occurring abundant species usually differ in lorica oral diameter. The graphs show the distribution of tintinnid species in size-classes of lorica oral diameter in March and October in contrasting systems: the Gullmar Fjord in western Sweden (Hedin 1974) and the Great Lagoon of New Caledonia (Dolan et al. 2006). In the Gullmar Fjord graphs, asterisks denote size-classes containing species described as abundant. In the New Caledonia graphs, numbers 1, 2, and 3 denote the size-classes of the first, second, and third most abundant species.

species was recorded. In general, within groups of ecologically similar organisms, occurrence is closely correlated with abundance, meaning the more often a species occurs in a set of samples, the higher its abundance relative to other species (Brown 1984; Gaston & He 2011). Overall, the winter and summer assemblages of tintinnids and *Ceratium* were surprisingly similar in species composition as well in the occurrence patterns of the species.

The tintinnid species catalogue for summer and winter combined numbered 112. Out of the 112, 64 were common to the summer and winter lists. Species found in the winter, but not in the summer, numbered but 14 of the 78 found. Of the 98 summer species, only 32 did not occur in the winter samples. Besides the large overlap in the lists of summer and winter species, species occurrences were also very similar. The most widespread species in the summer were, by and large, also widespread in winter (Table 10.3). The rank-occupancy patterns for the entire summer and winter assemblages (ranking each species in order of the portion of stations from which it was recorded) were

Table 10.3 Tintinnids of the Gulf of Mexico in winter and summer differed little in terms of the identities of the most abundant species: the 15 most widespread species in the summer and winter and their corresponding ranks in the two seasons (data extracted from Balech (1967a)); the most widespread summer species are denoted in bold.

Winter rank	Top 15 species Summer **and winter**	Summer rank
15	***Amphorides amphora***	1
10	***Amphorides quadrilineata***	11
6	***Ascampbelliella urceolata***	9
31	***Climacocylis scalaroides***	14
11	*Codonaria cistelula*	17
22	***Codonellopsis orthoceras***	15
13	*Dadayiella ganymedes*	16
2	***Dictyocysta lepida***	8
4	***Epiplocycloides reticulata***	4
36	***Epiplocylis undella***	6
27	***Eutintinnus fraknoii***	12
14	***Eutintinnus medius***	6
1	***Eutintinnus tenuis***	10
8	***Proplectella claparedei***	2
3	***Protorhabdonella simplex***	7
7	*Rhabdonella corncopia*	33
12	***Rhabdonellopsis apophysata***	3
9	*Steenstrupiella steenstrupi*	24
5	***Xystonella treforti***	13

similar log-normal or log-series patterns of a very few widespread species, and most species were found in fewer than 20% of the stations sampled (Fig. 10.24). The similarity of the summer and winter assemblages was also reflected in the correlation between a given species occurrence rank in the summer list and its occurrence rank in the winter list (Fig. 10.23).

The *Ceratium* species, which totaled 55 for summer and winter combined, showed the same overall patterns as the tintinnids when comparing the summer and winter assemblages. Most of the species were present in summer and winter samples. The summer assemblage of 49 species included only four not found in the winter samples. Of the 50 species in the winter assemblage, only six did not occur in the summer samples. The species occupancy patterns of the summer and winter assemblages were also similar, characterized by a very few widespread species and many species found in a minority of the stations sampled. Like tintinnid species, the occupancy ranks of a *Ceratium* species among the summer stations was

correlated with its occupancy rank in the winter assemblage but with a stronger correlation than that found with the tintinnids.

Overall, the assemblages of tintinnids and *Ceratium* in the Gulf of Mexico were nearly the same in the summer and in the winter. The apparent lack of a large seasonal change in assemblages contrasts with the studies of nearshore systems, whether temperate, subtropical, or tropical, all of which show marked differences. The apparent similarity of summer and winter species assemblages of both tintinnids and *Ceratium* could be the result of pooling data from several cruises sampling different areas, and thus an effect of sampling scale. Alternatively, stability of species assemblages may be an attribute of large open-water systems. Seasonality remains to be investigated in other open-water systems.

10.5   KEY POINTS

1. Global biogeography. Tintinnid geographic distributions at the generic level fall into one of five patterns: cosmopolitan, neritic, warm–temperate, boreal, and austral. These distributional patterns, or categories, roughly correspond to a modified latitudinal cosmopolitanism with a dichotomy between coastal and open-water forms. Although there are tintinnid genera with cosmopolitan distributions, no single species, or more precisely "morpho-species", is known to have a cosmopolitan distribution. In contrast, some species do show the very restricted distributions of endemics. The records of at least one species suggest recent artificial dispersal.

2. Distribution–abundance relationships. In common with many groups of organisms, there is a positive relationship between abundance and distribution among tintinnid species. Within a given system or biome, the population size of a species is positively related to its spatial and temporal occurrence. Conversely, rare species of tintinnids are both low in abundance as well as infrequently found.

3. Latitudinal diversity gradient. Tintinnids show a latitudinal gradient of species richness, one that is similar to that described for foraminifera and copepods. Thus, there may be a common "zooplankton latitudinal diversity gradient"; the pattern has been linked to average sea surface temperature, thought to reflect water column characteristics. The tintinnid pattern is also shared by dinoflagellates of the genus
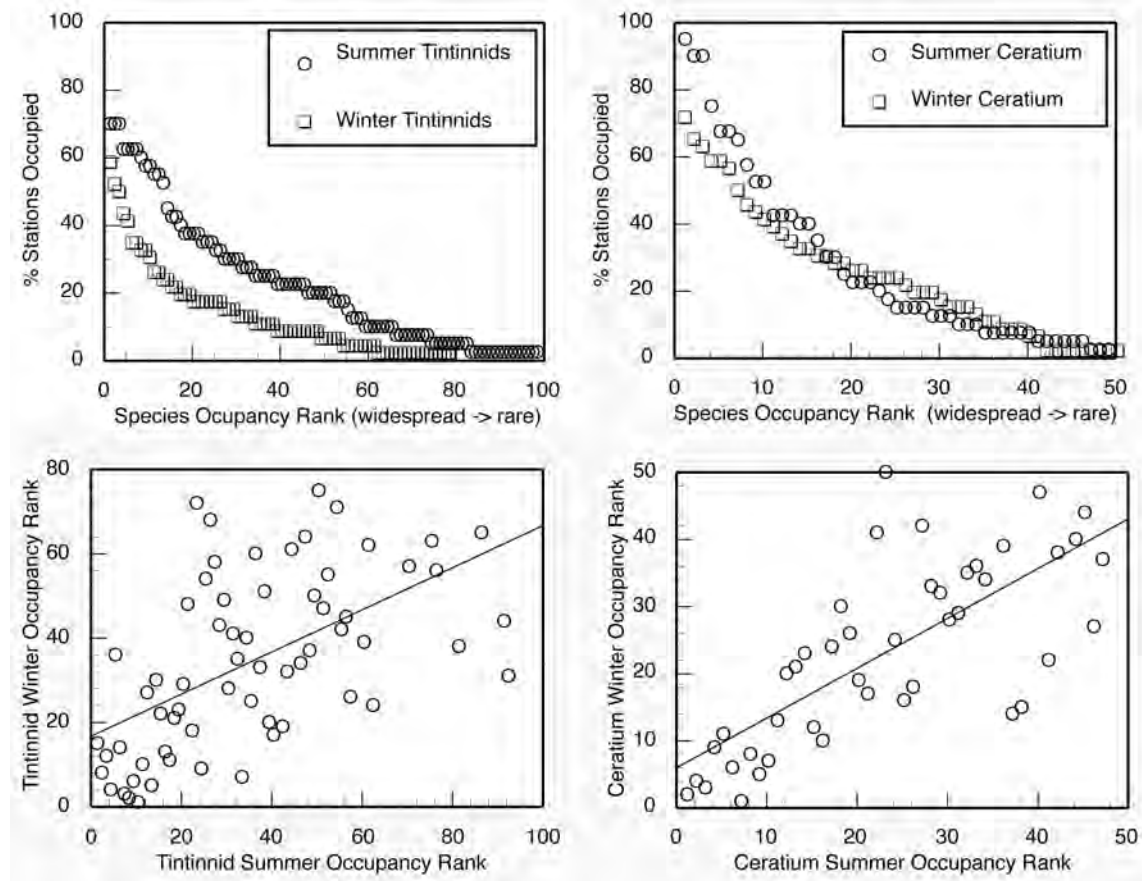
Fig. 10.24 Occupancy patterns of summer and winter assemblages of tintinnids and *Ceratium* in the Gulf of Mexico are both show little seasonal differences (based on data from Balech (1967a)). Top panels, geographic ranks, from widespread to rare, of each species in the summer and winter assemblages; bottom panels, the relationship between the geographic rank of species found both in the summer and winter. In summer, the most widespread tintinnid species, *Amphorides amphora*, was found in 70% of stations sampled; in winter, the most widespread species, *Eutintinnus tenue*, was found in about 60% of the stations sampled. All the species assemblages showed a pattern of species occupancy or occurrence of most species in just a few stations. For the species that occurred in both summer and winter, summer and winter ranks were significantly related (for tintinnids: $n = 64$, $r = 0.57$; for *Ceratium*: $n = 44$, $r = 0.74$).

Ceratium. However, different latitudinal gradients characterize other phytoplankton groups, diatoms, and coccolithophorids. As there appears to be no single latitudinal diversity gradient for marine plankton, different mechanisms likely act on different groups of the plankton.

4. Seasonal changes in species richness of coastal systems. Distinct seasonal patterns in the occurrences of individual species of tintinnids and species richness characterize most coastal ecosystems. A common pattern is species with hyaline loricae constitute the bulk of the community in the summer months whereas species with agglutinated loricae dominate during the remainder of the year. The period of highest species richness generally corresponds to periods of high overall tintinnid abundance. Within a coastal system,

patterns of seasonal changes in the species richness of tintinnids can parallel those of other planktonic groups such as aloricate ciliates, diatoms, or *Ceratium*, but can also be distinct.

5. Seasonal changes in morphotypes in coastal systems. In tintinnids the lorica oral diameter, which is relatively invariant for a given species, is related to the size of prey upon which the species feeds. In an assemblage, the most abundant species are usually of distinct oral diameters (compared with the other species present), presumably exploiting prey of distinct sizes. Various metrics of a "tintinnid community oral diameter" have been used to assess seasonal changes in community characteristics of tintinnid assemblages in terms of morphology, and seasonal changes in these metrics have been loosely related to changes in the characteristics of the phytoplankton crop.

6. Assemblages of open waters. Little is known of seasonal changes in tintinnid assemblages in open waters. However, it appears that open-water systems may lack the large seasonal change in assemblages known from coastal systems.
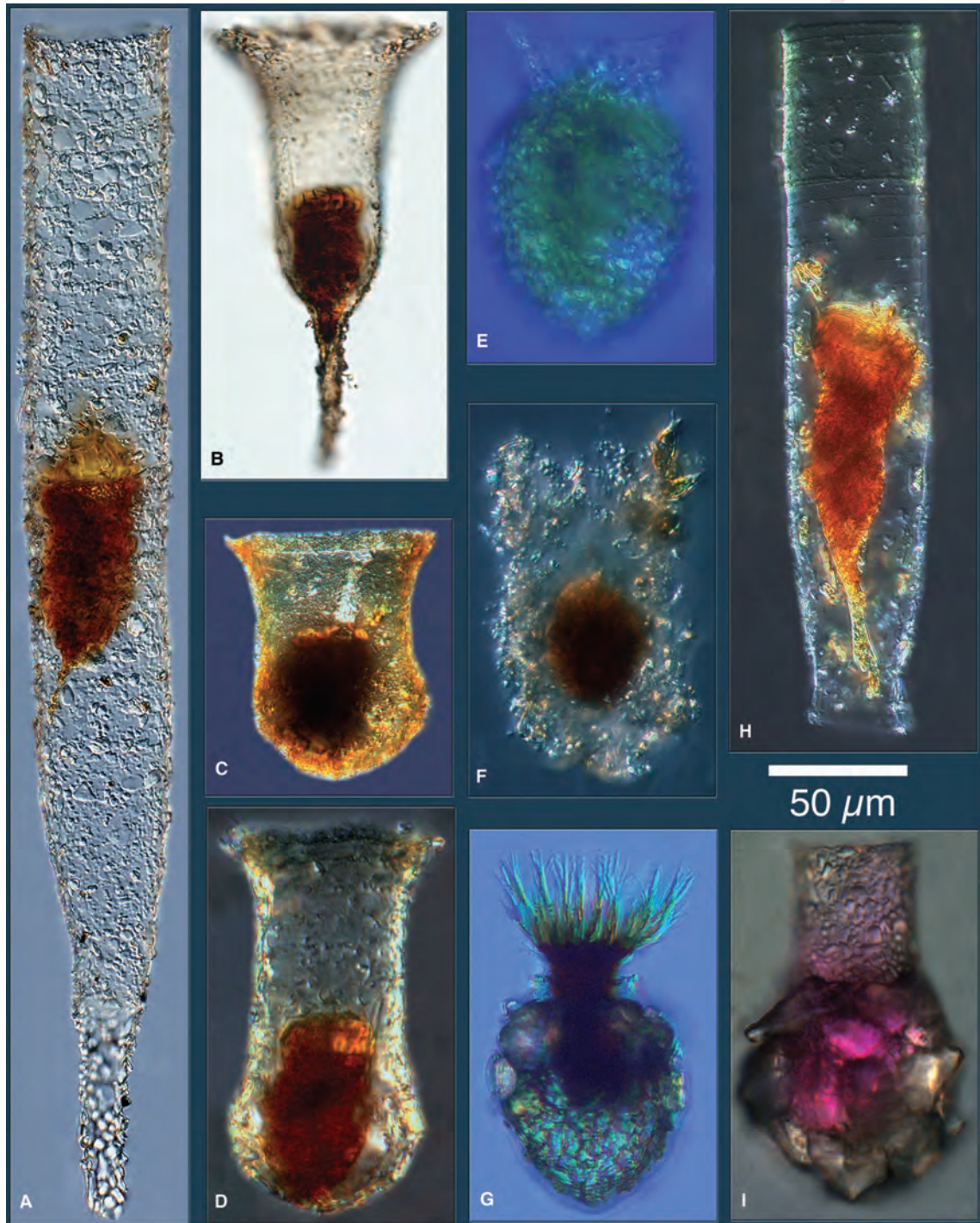
Plate 1.4 Some tintinnid species with agglutinated loricae: *Tintinnopsis radix* (a), *T. campanula* (b), *T. dadayi* (c), *T. spiralis* (d), *Codonella elongata* covered with coccoliths (e), *Tintinnidium* sp. (f), *Stenosomella ventricosa* (g), *Leprotintinnus pellucidus* (h), and *Codonellopsis schabi* (i). Species names are attributed based on lorica morphology. All the specimens are Lugol's-fixed cells except for *Codonella elongata* which was a live specimen.
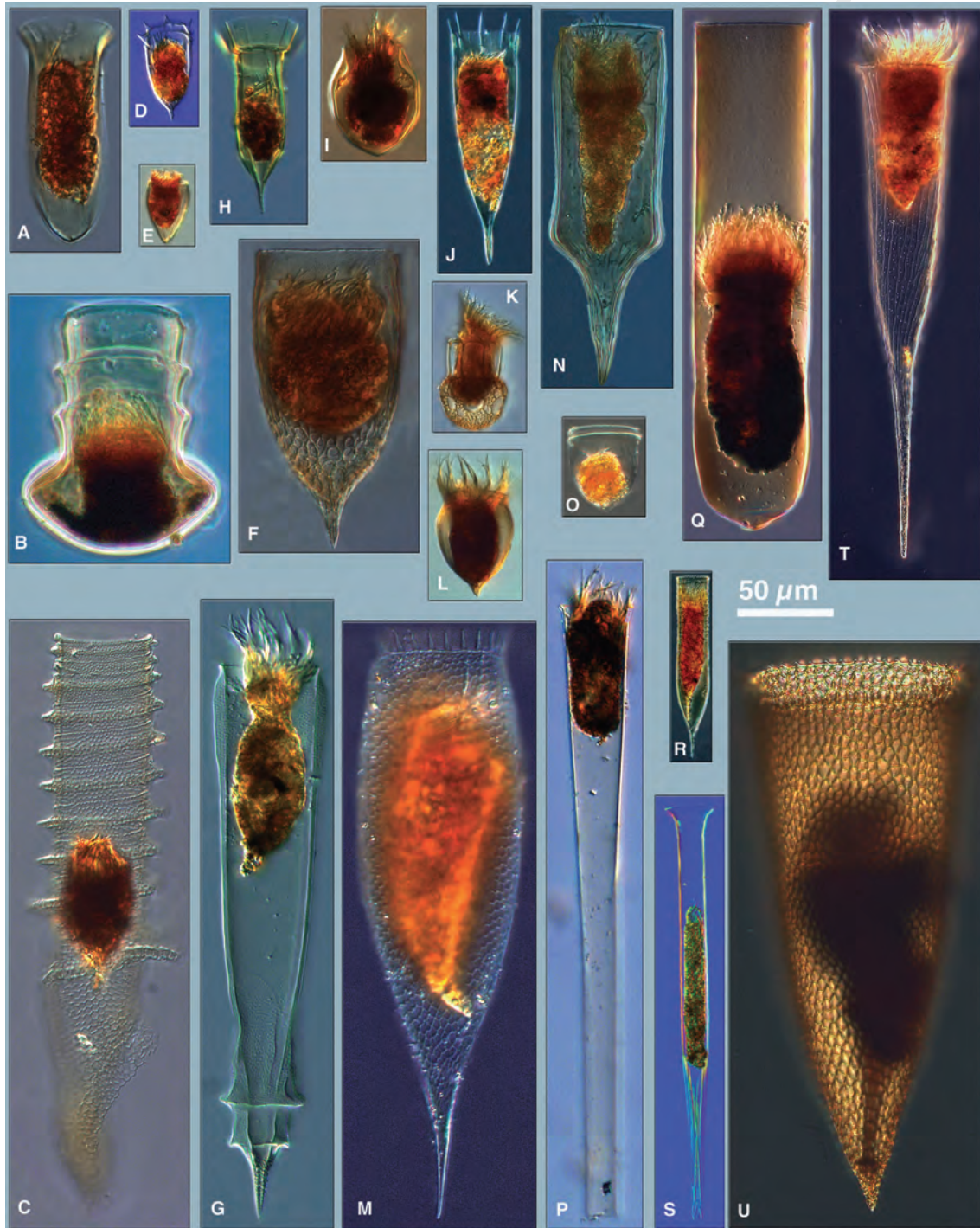
Plate 1.5 Examples of tintinnid species with hyaline loricae: *Amphorides quadrilineata* (a), *Amplectella collaria* (b), *Climacocylis scalaria* (c), *Acanthostomella conicoides* (d), *Protorhabdonella simplex* (e), *Epiplocylis blanda* (f), *Xystonellopsis paradoxa* (g), *Ormosella trachelium* (h), *Proplectella elipisoida* (i), *Dadayiella ganymedes* (j), *Dictyocysta lepida* (k), *Metacylis mediterranea* (l), *Parafavella parumdentata* (m), *Parundella messinensis* (n), *Ascampbellia tortulata* (o), *Eutintinnus stramentus* (p), *Undella hyalina* (q), *Helicostomella subulata* (r), *Salpingella acuminata* (s), *Rhabdonella spiralis* (t), and *Cyttarocylis cassis* (u). All the specimens are Lugol's-fixed cells.
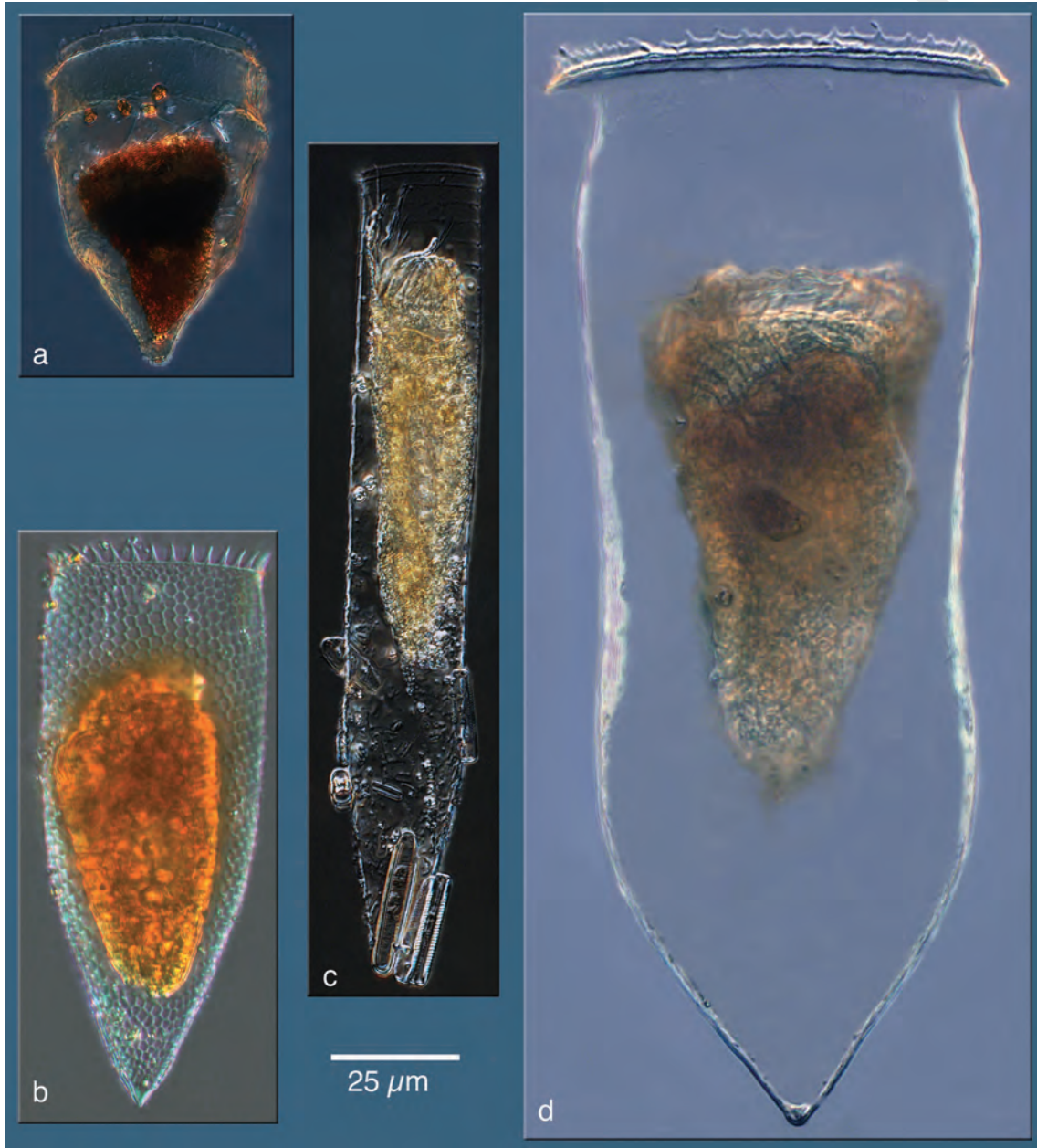
Plate 10.1 Examples of species with distributions restricted to high latitudes. *Ptychocylis acuta* (a) and *Parafavella parumdendata* (b) are found only in Arctic and Subarctic waters while *Laackmanniella prolongata* (c) and *Cymatocylisdrygalskii* (d) are restricted to Antarctic waters.
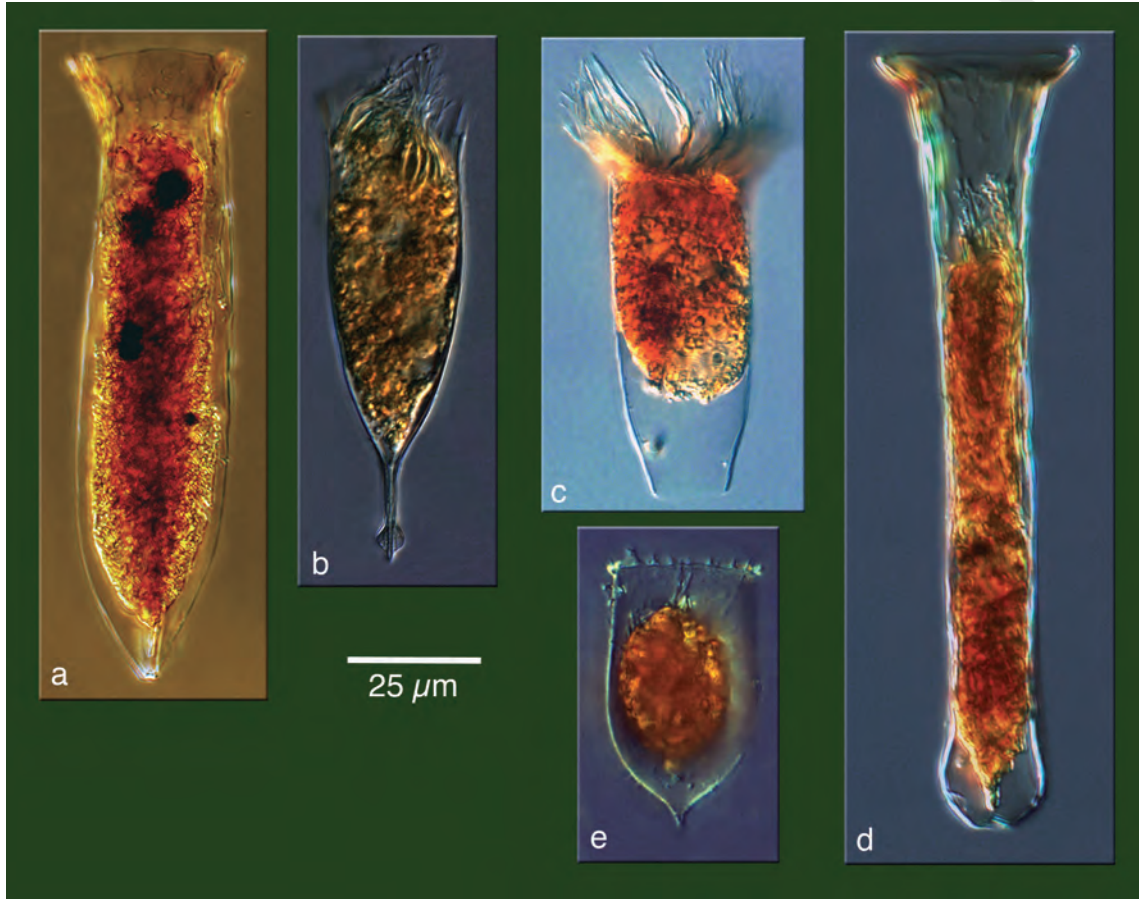
Plate 10.2 The most commonly reported and widely distributed tintinnid species. *Amphorides quadrilineata* (a) specimen from the Scripps Canyon area in the Pacific Ocean; *Dadayiella ganymedes* (b) from the Indian Ocean collected during the Tara Oceans Expedition; *Eutintinnus apertus* (c) and *Steenstrupiella steenstrupii* (d) both from the Bay of Villefranche in the N.W. Mediterranean Sea; *Acanthostomella norvegica* (e) from the Bering Sea. All specimens were preserved with Lugol's solution.