

# Phytoplankton community ecology: principles applied in San Francisco Bay

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**ABSTRACT:** In his seminal 1961 paper 'The paradox of the plankton' *Am Nat* 95:137–147, G. E. Hutchinson asked why many species of phytoplankton can coexist while competing for a small number of limiting resources in an unstructured habitat. Hutchinson anticipated the resolution of his paradox, recognizing that communities are organized by processes beyond resource competition including species interactions, habitat variability and dispersal. Since 1961 we have made fundamental discoveries that have revolutionized our conceptual understanding of pelagic ecology, including (1) habitat heterogeneity at all scales relevant to plankton population dynamics, (2) community shifts in response to global climate cycles, (3) fast and selective predation as a powerful top-down force to shape phytoplankton communities, (4) turbulent mixing as a physical process that selects species on the basis of their size and form, (5) mixotrophy that allows some algal species to tap organic nutrient pools and function at multiple trophic levels, (6) taxon-specific life cycles including alternating vegetative and resting stages, and (7) the pelagic as an open system where communities are continually reshaped by species immigration. Here we synthesize these discoveries to show how they validate and amplify Hutchinson's hypothesis that phytoplankton communities are assembled by many processes. Our synthesis is built around observations of phytoplankton species composition from a decade of study in San Francisco Bay, used as a case study to illustrate the contemporary principles of phytoplankton community ecology. We apply these principles to address 2 central questions: (1) What processes assemble phytoplankton communities? (2) How does phytoplankton community composition influence ecosystem functions such as production in pelagic and benthic food webs?

**KEY WORDS:** Phytoplankton · Community ecology · Ecosystem functions · Aquatic ecosystems · Food webs · Biological diversity · Paradox of the plankton

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## INTRODUCTION

The challenge of deciphering the rules of phytoplankton community assembly remains a central problem of aquatic ecology. Phytoplankton photosynthesis fixes up to 50 Gt of carbon per year, contributing nearly half of global primary production (Falkowski et al. 1998). The biogeochemical consequences and fate of that production are determined by the way in which it is packaged into species having distinct biochemical contents and cell sizes spanning 6 orders of magnitude. Diatom production is a net sink for CO<sub>2</sub>, whereas coccolithophorid production is a net source, so community composition at this level determines the direction of

ocean–atmosphere CO<sub>2</sub> exchange, with corresponding influence on the climate system (Harrison 2000). Micron-sized picoplankton are not directly accessible to most metazoan consumers (Tamineaux et al. 1995), so their energy content is routed through the microbial loop, with large respiratory losses. Some algal taxa synthesize biochemicals that are essential dietary components for animal consumers (Müller-Navarra et al. 2004), while others produce potent toxins to disrupt animal growth or reproduction (Cembella 2003). The pathways and efficiencies of energy transfer from primary producers to aquatic food webs, including those sustaining upper trophic levels, are therefore determined by phytoplankton community composition.

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In his seminal paper 'The paradox of the plankton', Hutchinson (1961) asked how 'is it possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials'? The paradox was coexistence of many species when the competitive exclusion principle predicts 'that one species alone would out compete all the others so that in a final equilibrium situation the assemblage would reduce to a population of a single species.' The paradox was grounded on assumptions that: (1) phytoplankton communities are assembled on the basis of differential growth rates among species, determined by the availability of inorganic nutrients, (2) species interact through competition for mineral nutrients, and (3) pelagic habitats are homogeneous closed systems. In the 4 decades since, our concepts of pelagic ecology have been revolutionized by fundamental new discoveries that resolve the paradox, largely through confirmation of mechanisms anticipated by Hutchinson (1961): species immigration, biological interactions, and habitat variability that precludes community equilibrium.

Here, we synthesize those discoveries and their contribution to the revolutionized view of pelagic ecology since Hutchinson's era. We build this synthesis with examples of species occurrence and distributional patterns from a decade-long survey of phytoplankton communities in San Francisco Bay. We use this case study as a foundation to synthesize important discoveries since Hutchinson's paper to address 2 fundamental ecological questions: (1) What are the patterns and processes of phytoplankton community assembly in open ecosystems such as estuaries and oceanic current systems? and (2) How does phytoplankton community composition influence ecosystem functions such as food supply to consumers and energy transfer to pelagic and benthic food webs?

## MATERIALS AND METHODS

**San Francisco Bay: the case study.** San Francisco Bay, the estuary between California's 2 largest rivers and the Pacific Ocean, is a site of long-term ecological research designed to reveal patterns and processes of variability in a coastal ecosystem (Cloern 1996). Estuaries are open systems strongly influenced by river inflows, mixing with the coastal ocean, and exchanges across the sediment–water interface that drive physical and biogeochemical variability. Estuaries are turbulent advective systems in which the pelagic and its biota are dispersive and transient. Their pelagic habitats are time-varying mixtures of seawater and freshwater, situated within spatial gradients of salinity, temperature, nutrients, turbidity and heterotroph communities along a river–ocean continuum. Long-term

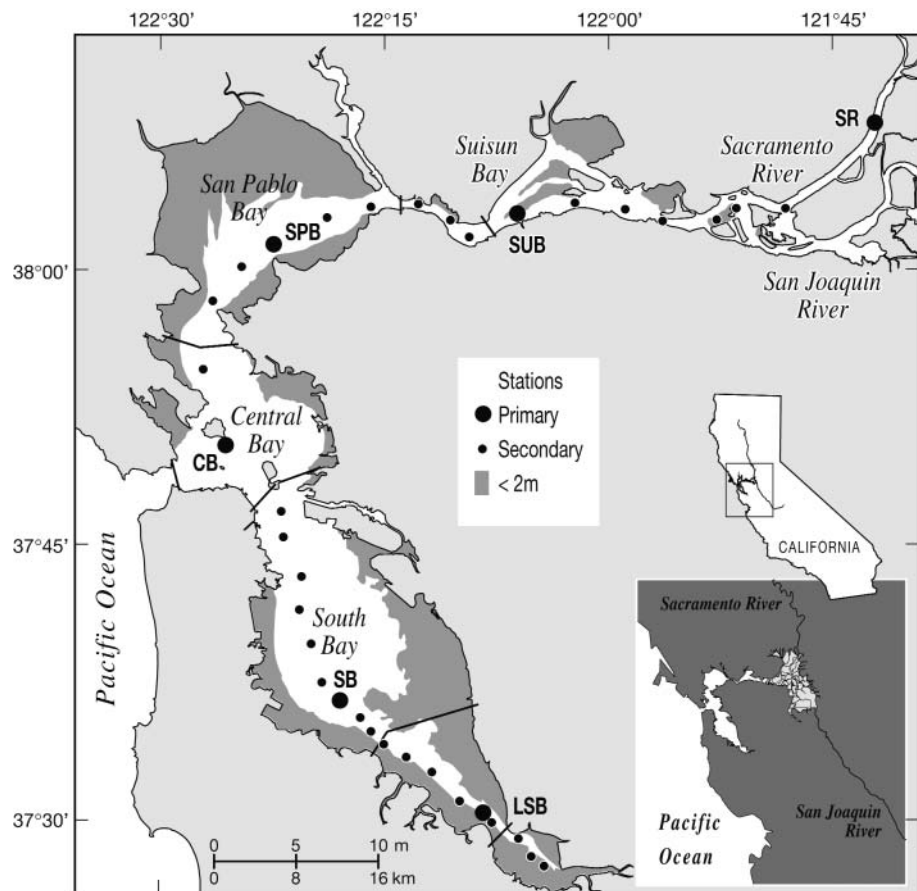
observations across the habitat gradients of San Francisco Bay provide an appropriate data set for illustrating principles that have emerged from the discovery of processes beyond resource competition that shape phytoplankton communities.

**Methods.** For a decade (1992 to 2001), we sampled seasonally along the salinity gradients of San Francisco Bay between the tidal freshwater Sacramento River, marine-influenced Central Bay, and brackish-marine South San Francisco Bay (Fig. 1). We measured salinity, temperature, irradiance, phytoplankton biomass as chlorophyll *a*, suspended sediment and dissolved inorganic nutrient (N, P, Si) concentrations to capture variability associated with annual cycles of river flow and biomass and activity of herbivores (Cloern 1996). Phytoplankton samples were collected within the 6 sub-regimes of the river-estuary system (Fig. 1), identified from tree-based regressions of chlorophyll distributions (Jassby et al. 1997). These 6 primary stations were sampled during spring 1992 and then roughly bimonthly each year from 1993 through 2001 (see Fig. 2E). Additional (ca. weekly) samples were collected in South Bay when the biomass fluctuated around neap-spring periodicity of tidal mixing.

Vertical profiles of temperature, salinity and photosynthetically active radiance ( $I_z$ ) were measured with a Seabird Electronics CTD and LiCor 192 quantum sensor. The light-attenuation coefficient  $k$  was calculated as the slope of linear regression of  $\ln(I_z)$  against depth  $z$ . Vertical distributions of suspended particulate matter (SPM) and chlorophyll *a* were measured with a D&A Instruments optical backscatter sensor and Sea-Tech fluorometer calibrated with discrete measures of SPM and chlorophyll *a* in near-surface and near-bottom water samples. Chlorophyll *a* samples were filtered onto Gelman A/E glass-fiber filters and frozen. Dried filters were ground in 90% acetone, extracted in a freezer for 24 h, and the absorbance of centrifuged extracts measured with a Hewlett Packard 8452A diode-array spectrophotometer. Chlorophyll *a* concentration was calculated using Lorenzen's (1967) equations with corrections for phaeopigments. SPM was determined gravimetrically using samples collected onto pre-weighed Nuclepore (0.4  $\mu\text{m}$  pore size) filters. From 1992 through 2001, we measured 4118 vertical profiles along the river–estuary transect. We present (Fig. 2) only measurements at 1 m depth, corresponding to the depth of phytoplankton sampling.

Nutrient samples were filtered through 0.4  $\mu\text{m}$  Nuclepore filters and frozen until analyzed. Concentrations of dissolved inorganic nitrogen ( $\text{DIN} = \text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$ ), reactive phosphorus and silica were measured using modifications of standard colorimetric methods (Hager & Schemel 1997) with a Technicon AutoAnalyzer II. We computed indices of nutrient

Fig. 1. Sampling locations in San Francisco Bay (●). Vertical profiles of chlorophyll *a*, suspended particulate matter, irradiance, temperature, and salinity were measured at all stations. Phytoplankton and nutrient samples were collected at the primary stations distributed among 6 subregions along the salinity gradient. Data are available at <http://sfbay.wr.usgs.gov/access/wqdata>



limitation as measured concentrations normalized by half-saturation constants for growth ( $K$ ), assuming that  $K_N = 0.7 \mu\text{M}$ ,  $K_P = 0.1 \mu\text{M}$ ,  $K_{Si} = 1.8 \mu\text{M}$  (Chapra 1997). We computed an index of light limitation as mean water-column irradiance [ $= E/(kH)$ , where  $H$  is water depth and  $E$  is daily surface irradiance], scaled by a characteristic irradiance at which growth rate is half the maximum ( $K_I = 2.4 \text{ mol quanta m}^{-2} \text{ d}^{-1}$ ; Cloern 1999).

Phytoplankton samples were preserved with acid Lugol's solution, and 2 to 50 ml aliquots were settled in chambers for 6 to 24 h, and then counted and identified using a phase-contrast inverted microscope (Utermöhl 1958). Entire aliquots were examined at 125 $\times$  magnification and all cells  $>30 \mu\text{m}$  diameter were enumerated. Cells smaller than  $30 \mu\text{m}$  were counted at 1250 $\times$  magnification; at least 100 cells of the most numerous taxon were counted using the strip-count method (APHA 1989). Diatoms and dinoflagellates were identified after the cell contents were cleared in 30% hydrogen peroxide and mounted in Hyrax Mounting Medium. Cell volumes were estimated for dominant taxa by measuring 50 to 100 cells (Hillebrand et al. 1999) and applying the geometric formulas of Wetzel & Likens (1991). The biomass of each taxon was computed as the product of abundance (cells  $\text{ml}^{-1}$ ) and cell biovolume ( $\mu\text{m}^3 \text{ ml}^{-1}$ ).

From mean cell dimensions we computed the size of each species as equivalent spherical diameter (ESD).

**San Francisco Bay as a habitat mosaic.** Phytoplankton communities were sampled across a mosaic of physical–chemical habitats, where the variability of salinity (0.05 to 32.2 psu), temperature (8.7 to 22.7°C), turbidity (SPM from 1 to 556  $\text{mg l}^{-1}$ ) and nutrient concentrations (dissolved inorganic nitrogen, DIN, from 0.05 to 221  $\mu\text{M}$ ) reflected a broad range of environmental factors that regulate phytoplankton growth (Fig. 2). Hydrologic conditions ranged from seasonal low riverine inflow of  $\sim 100 \text{ m}^3 \text{ s}^{-1}$  during summer and autumn to exceptional flood events ( $>9000 \text{ m}^3 \text{ s}^{-1}$ , Fig. 2A). The salinity distribution responded with rapid estuary-wide displacements of seawater and its plankton community during periods of high inflow followed by progressive salinity intrusion during the low flow in summer and autumn (Fig. 2C). Spatial distributions of SPM (Fig. 2D) created large river–ocean gradients in turbidity and light limitation of phytoplankton growth. Most samples had chlorophyll *a* concentrations  $<3 \mu\text{g l}^{-1}$ . Exceptions occurred as blooms, mostly in South Bay (Fig. 2E), when chlorophyll *a* exceeded  $20 \mu\text{g l}^{-1}$  and reached maxima  $>100 \mu\text{g l}^{-1}$ . DIN, Si and P usually exceeded concentrations that limit phytoplankton

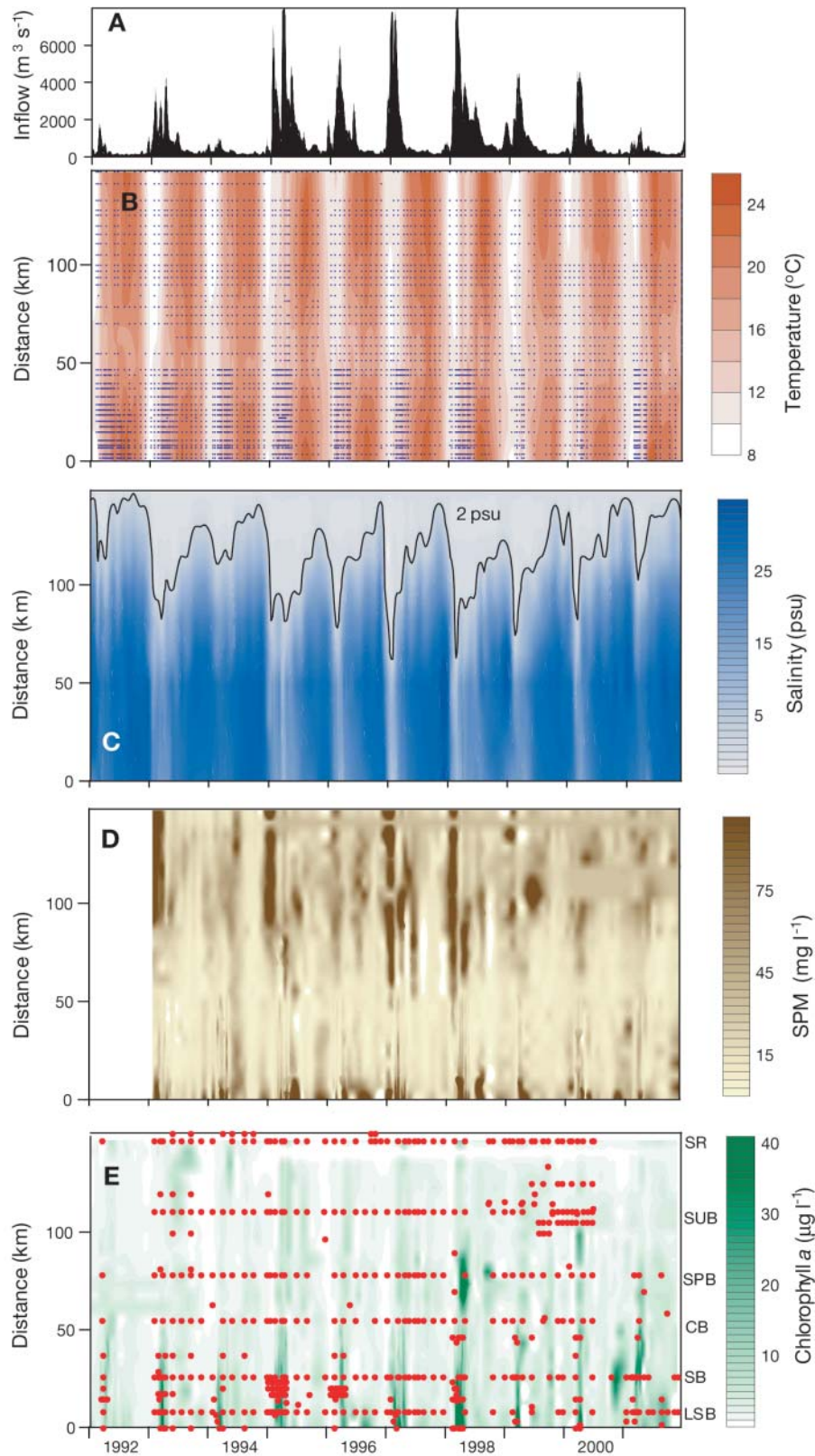


Fig. 2. Daily (A) river inflow and color contours showing interpolated distributions of near-surface: (B) water temperature, (C) salinity, (D) suspended particulate matter (SPM), and (E) chlorophyll *a* concentration along the San Francisco Bay sampling transect from 1992 to 2001. In (B), blue symbols identify times and locations of 4118 measurements of temperature, salinity, SPM, and chlorophyll *a*. In (E), red circles identify times and locations where phytoplankton samples were collected for microscopic analysis. Primary sampling sites were Lower South Bay (LSB), South Bay (SB), Central Bay (CB), San Pablo Bay (SPB), Suisun Bay (SUB), and Sacramento River (SR) (see Fig. 1 for locations)

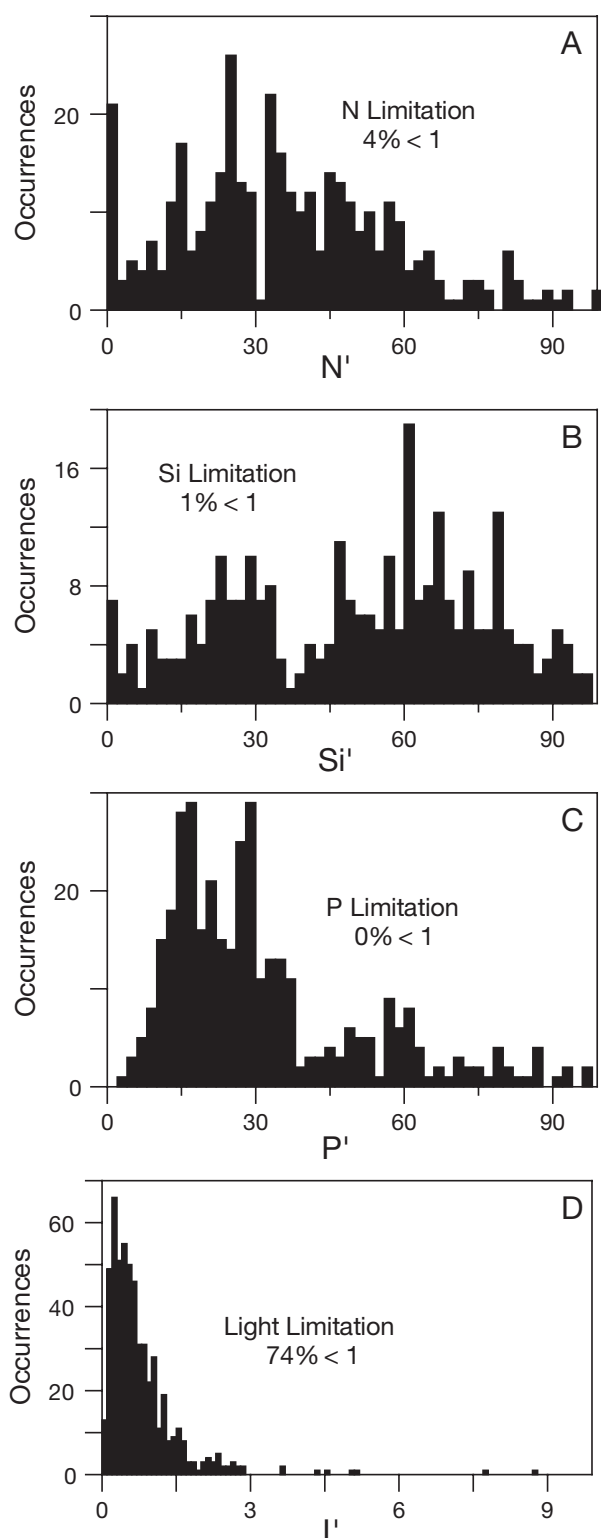


Fig. 3. Frequency distributions (number of occurrences) of nutrient (N, Si, P) concentrations and water-column irradiance ( $I$ ), measured in San Francisco Bay from 1992 to 2001. Measurements were normalized to half-saturation constants defining resource limitation of phytoplankton growth. Note difference in x-axis scale between (A–C) and (D)

growth. Scaled concentrations of DIN ( $N' = \text{DIN}/K_N$ ) indicate that phytoplankton growth was potentially limited by N ( $N' < 1$ ) in only 4% of samples (Fig. 3). Si was at rate-limiting concentrations for diatoms ( $Si' < 1$ ) in only 1% of samples, and P limitation was never indicated. Irradiance profiles indicated light limitation of growth in 74% of samples (Fig. 3D), confirming that phytoplankton growth is predominately limited by the light resource in this enriched estuary (Cloern 1999).

**Phytoplankton community of San Francisco Bay.** We detected 500 distinct phytoplankton taxa, of which 396 could be identified to species. Accurate enumeration and identification of prokaryotes and some small eukaryotic algae is not possible by light microscopy, and some fragile taxa (e.g. the raphidophyte *Heterosigma akashiwo*) can only be detected in live samples. Therefore, our analysis of size and taxonomic diversity is constrained to those forms that were well-preserved and identifiable by light microscopy. Of these taxa, cell volume ranged from 1 to 3  $\mu\text{m}^3$  for the smallest taxa (*Nannochloropsis* sp., *Chromulina mikroplankton*, *Merismopedia* spp., *Aphanocapsa* spp.) to 4–6  $\times 10^5 \mu\text{m}^3$  for the largest (*Coscinodiscus centralis* var. *pacifica*, *Thalassiosira anguste-lineata*, *Coscinodiscus oculus-iridis*, *Noctiluca scintillans*). We compiled mean cell size for the 81 most important species (Table 1), a community of cosmopolitan phytoplankton commonly observed in temperate estuaries and coastal waters globally.

The phytoplankton community was dominated by a small number of species: the top 10 contributed 77% to cumulative biomass in the 599 samples, and the top 100 species contributed >99% (Fig. 4A). Diatoms (division Bacillariophyta) contributed 81% to cumulative biomass in all samples (Fig. 4B). Dinoflagellates (Pyrophyta) and cryptophytes contributed 11 and 5%, respectively, to cumulative biomass. Other divisions (Chlorophyta, Cyanophyta, Chrysophyta, Euglenophyta) were minor components of overall biomass, although their contributions were important in some individual samples. We probed the San Francisco Bay data set to extract patterns illustrating principles of phytoplankton community assembly that have emerged from discoveries since Hutchinson's era.

## RESULTS AND DISCUSSION

### Eight principles of phytoplankton community assembly

**(1) Cell size is determined by nutrient supply and selective grazing:** Major conceptual breakthroughs of pelagic ecology have come from discoveries of the microbial loop (Pomeroy 1974, Azam et al. 1983) and the distinction between new and regenerated produc-

Table 1. Common phytoplankton taxa in San Francisco Bay, listing those species occurring in >10 (of 599) samples and contributing >0.01% of cumulative biomass as biovolume contained in all samples. Mean cell size as equivalent spherical diameter (ESD). n = no. of occurrences

Taxon	Division	Biomass (%)	ESD (µm)	n
<i>Thalassiosira rotula</i> Meunier	Bacillariophyta	20.97	28	140
<i>Chaetoceros socialis</i> Lauder	Bacillariophyta	11.98	12	48
<i>Skeletonema costatum</i> (Greville) Cleve	Bacillariophyta	9.51	8	277
<i>Ditylum brightwellii</i> (T. West) Grunow	Bacillariophyta	7.44	85	103
<i>Gymnodinium sanguineum</i> Hirasaka	Pyrrophyta	7.40	61	41
<i>Coscinodiscus oculus-iridis</i> Ehrenberg	Bacillariophyta	6.30	101	66
<i>Thalassiosira hendeyi</i> Hasle & Fryxell	Bacillariophyta	4.85	51	203
<i>Thalassiosira punctigera</i> (Castracane) Hasle	Bacillariophyta	3.31	72	27
<i>Plagioselmis prolunga</i> var. <i>nordica</i> Novarino, Lucas & Morrall	Cryptophyta	2.65	5	495
<i>Coscinodiscus curvatulus</i> Grunow	Bacillariophyta	2.15	73	49
<i>Mesodinium rubrum</i> Lohmann	Holotrich ciliate	2.03	30	190
<i>Teleaulax amphioxeia</i> (Conrad) Hill	Cryptophyta	2.02	9	375
<i>Chaetoceros debilis</i> Cleve	Bacillariophyta	1.84	11	31
<i>Eucampia zodiacus</i> Ehrenberg	Bacillariophyta	1.80	30	29
<i>Coscinodiscus radiatus</i> Ehrenberg	Bacillariophyta	1.77	53	66
<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve	Bacillariophyta	1.48	55	136
<i>Protoperidinium</i> sp.	Pyrrophyta	1.45	37	21
<i>Thalassiosira decipiens</i> (Grunow) Jorgensen	Bacillariophyta	0.90	20	136
<i>Coscinodiscus centralis</i> var. <i>pacifica</i> Gran & Angst	Bacillariophyta	0.72	103	23
<i>Rhizosolenia setigera</i> Brightwell	Bacillariophyta	0.49	29	102
<i>Noctiluca scintillans</i> (Macartney) Kofoid & Swezy	Pyrrophyta	0.46	98	36
<i>Nitzschia bilobata</i> W. Smith	Bacillariophyta	0.44	35	33
<i>Cyclotella atomus</i> Hustedt	Bacillariophyta	0.43	7	304
<i>Coscinodiscus jonesianus</i> (Greville) Ostensfeld	Bacillariophyta	0.33	68	17
<i>Pyramimonas orientalis</i> Butcher	Chlorophyta	0.31	5	175
<i>Rhodomonas marina</i> (Dangeard) Lemmermann	Cryptophyta	0.26	10	116
<i>Protoperidinium depressum</i> (Bailey) Balech	Pyrrophyta	0.23	60	41
<i>Heterocapsa triquetra</i> (Ehrenberg) Stein	Pyrrophyta	0.23	18	138
<i>Protoperidinium claudicans</i> (Paulsen) Balech	Pyrrophyta	0.22	26	52
<i>Cyclotella choctawhatcheeana</i> Prasad	Bacillariophyta	0.22	12	74
<i>Alexandrium tamarense</i> (Lebour) Balech	Pyrrophyta	0.21	23	109
<i>Nannochloropsis</i> sp.	Chrysophyta	0.20	2	424
<i>Thalassiosira nodulolineata</i> (Hendey) Hasle & Fryxell	Bacillariophyta	0.18	49	40
<i>Chlorella salina</i> Butcher	Chlorophyta	0.17	3	97
<i>Chaetoceros wighamii</i> Brightwell	Bacillariophyta	0.17	9	43
<i>Eutreptia lanowii</i> Steur	Euglenophyta	0.16	11	167
<i>Prorocentrum minimum</i> (Pavillard) Schiller	Pyrrophyta	0.16	14	116
<i>Aulacoseira lirata</i> (Ehrenberg) Ross	Bacillariophyta	0.15	12	12
<i>Rhizosolenia styliiformis</i> Brightwell	Bacillariophyta	0.13	48	22
<i>Entomoneis paludosa</i> (W. Smith) Reimer	Bacillariophyta	0.12	28	30
<i>Odontella mobiliensis</i> (Bailey) Grunow	Bacillariophyta	0.11	71	17
<i>Gyrosigma balticum</i> (Ehrenberg) Rabenhorst	Bacillariophyta	0.11	53	36
<i>Pleurosigma strigosum</i> W. Smith	Bacillariophyta	0.09	32	61
<i>Leptocylindrus minimus</i> Gran	Bacillariophyta	0.09	11	36
<i>Gyrodinium spirale</i> (Bergh) Kofoid & Swezy	Pyrrophyta	0.09	51	21
<i>Thalassiosira visurgis</i> Hustedt	Bacillariophyta	0.08	21	50
<i>Oxytoxum milneri</i> Murray & Whitting	Pyrrophyta	0.08	28	75
<i>Lithodesmium undulatum</i> Ehrenberg	Bacillariophyta	0.08	69	14
<i>Gyrosigma fasciola</i> (Ehrenberg) Griffith & Henfrey	Bacillariophyta	0.08	32	91
<i>Cyclotella striata</i> (Kuetzing) Grunow	Bacillariophyta	0.08	13	63
<i>Heterocapsa rotundata</i> (Lohmann) Hansen	Pyrrophyta	0.07	11	94
<i>Pyramimonas disomata</i> Butcher	Chlorophyta	0.07	14	112
<i>Chaetoceros subtilis</i> Cleve	Bacillariophyta	0.07	7	57
<i>Chaetoceros gracilis</i> Schutt	Bacillariophyta	0.05	7	23
<i>Asterionellopsis glacialis</i> (Castracane) Round	Bacillariophyta	0.05	20	33
<i>Guinardia delicatula</i> (Cleve) Hasle	Bacillariophyta	0.05	21	100
<i>Chlorella marina</i> Butcher	Chlorophyta	0.05	5	86
<i>Paralia sulcata</i> (Ehrenberg) Cleve	Bacillariophyta	0.05	13	166
<i>Actinoptychus senarius</i> Ehrenberg	Bacillariophyta	0.05	58	39

Table 1 (continued)

Taxon	Division	Biomass (%)	ESD ( $\mu\text{m}$ )	n
<i>Pleurosigma normanii</i> Ralfs	Bacillariophyta	0.04	47	17
<i>Pseudo-nitzschia seriata</i> (Cleve) Peragallo	Bacillariophyta	0.04	15	34
<i>Cyclotella meneghiniana</i> Kuetzing	Bacillariophyta	0.04	13	57
<i>Gyrosigma acuminatum</i> (Kuetzing) Rabenhorst	Bacillariophyta	0.04	42	24
<i>Melosira varians</i> Agardh	Bacillariophyta	0.03	22	26
<i>Nitzschia pusilla</i> Grunow	Bacillariophyta	0.03	7	69
<i>Alexandrium catenella</i> (Whedon & Kofoid) Balech	Pyrrophyta	0.03	26	22
<i>Ceratium furca</i> (Ehrenberg) Claparede & Lachmann	Pyrrophyta	0.03	41	11
<i>Thalassiosira nordenskiöldii</i> Cleve	Bacillariophyta	0.03	16	40
<i>Gyrosigma macrum</i> (W. Smith) Griffith & Henfrey	Bacillariophyta	0.03	31	71
<i>Stephanodiscus hantzschii</i> Grunow	Bacillariophyta	0.03	11	11
<i>Prorocentrum micans</i> Ehrenberg	Pyrrophyta	0.02	30	29
<i>Scrippsiella hangoei</i> (Schiller) Larsen	Pyrrophyta	0.02	32	18
<i>Prorocentrum gracile</i> Schutt	Pyrrophyta	0.02	20	17
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen	Bacillariophyta	0.02	14	32
<i>Synechocystis salina</i> Wislouch	Cyanophyta	0.02	2	61
<i>Aulacoseira italica</i> (Ehrenberg) Simonsen	Bacillariophyta	0.02	13	18
<i>Protoperdinium bipes</i> (Paulsen) Balech	Pyrrophyta	0.02	22	43
<i>Nitzschia closterium</i> (Ehrenberg) W. Smith	Bacillariophyta	0.02	7	122
<i>Nitzschia longissima</i> (Brebisson) Ralfs	Bacillariophyta	0.02	11	143
<i>Thalassionema nitzschioides</i> (Grunow) Mereschkowsky	Bacillariophyta	0.02	13	47
<i>Cryptomonas ovata</i> Ehrenberg	Cryptophyta	0.02	15	27

tion (Dugdale & Goering 1967). We know now that phytoplankton biomass and production are dominated by micron-sized picoplankton in oligotrophic lakes and much of the ocean. Small size (high surface:volume ratio) provides a competitive advantage in nutrient-impooverished regenerating systems (Chisholm 1992), but this advantage disappears in new-production systems when physical processes inject nutrients into the

euphotic zone and promote selective growth of large cells that escape predation by fast-responding microheterotrophs (Kjørboe 1993). As predicted from this principle, phytoplankton biomass in the nutrient-rich San Francisco Bay is dominated by large taxa: cells  $<8 \mu\text{m}$  contributed only 4 % of community biomass, but cells  $>30 \mu\text{m}$  contributed 40 % (Fig. 4B). This is consistent with an earlier study demonstrating that ultra-

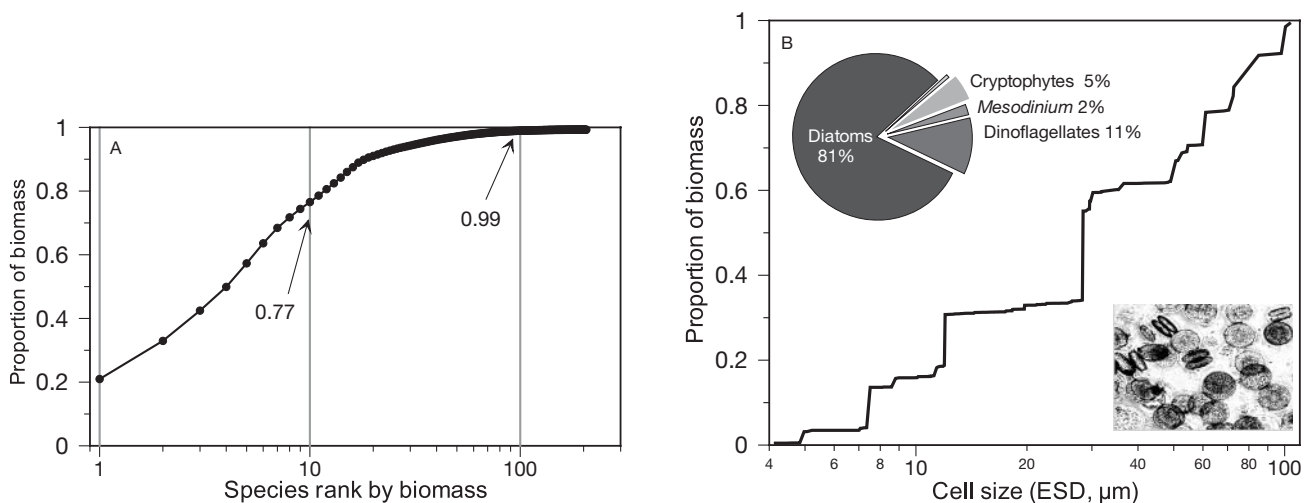


Fig. 4. (A) Cumulative distribution of total phytoplankton biomass in 599 samples versus number of species included, ranked by biomass; 10 most important species contributed 77 % of cumulative biomass, and 100 species accounted for  $>99\%$  of cumulative biomass. (B) Cumulative frequency distribution of phytoplankton biomass versus cell size (ESD, equivalent spherical diameter); top inset shows relative contributions to total biomass by diatoms, dinoflagellates, cryptophytes and phototrophic ciliate *Mesodinium rubrum*. Photomicrograph inset shows a sample collected during a spring diatom bloom dominated by *Thalassiosira punctigera* having mean diameter  $\sim 90 \mu\text{m}$

plankton (cells passing a 5  $\mu\text{m}$  filter) contributed only 3 to 28% to chlorophyll biomass and annual primary production in different regions of San Francisco Bay (Cole et al. 1986). Much of the large-cell production occurred during blooms, when biomass was dominated by *Thalassiosira rotula*, *T. hendeyi*, *T. punctigera*, *Chaetoceros socialis*, *C. debilis*, *Skeletonema costatum*, *Ditylum brightwellii*, *Coscinodiscus oculus-iridis*, *C. curvatulus*, *C. radiatus* and *Eucampia zodiacus* (Table 1). Analyses by epifluorescence microscopy (Ning et al. 2000) confirmed that picoplankton (primarily cyanobacteria *Synechococcus* spp.) contributed about 15% to community biomass during nonbloom conditions and only 2% during blooms. Phytoplankton dynamics in upwelling systems and many estuaries are characterized by boom–bust cycles of large cells against a background of stable picoplankton biomass (Cullen et al. 2002). The damped biomass fluctuations of small cells result from tight coupling between their production and consumption by fast-responding protists (Murrell & Hollibaugh 1998). As a consequence of fast grazing in the microbial loop and lagged responses of metazoan consumers (Malone 1992), nutrient enrichment amplifies large-cell production (Duarte et al. 2000).

**(2) Diatoms respond rapidly to nutrient pulses:** The phytoplankton community of San Francisco Bay is overwhelmingly dominated by diatoms (Fig. 4B), a result of dominance during blooms when their cell-division rate exceeds loss rates from grazing, sedimentation, transport and mortality. Large diatoms are key species in this estuary just as they are in the ocean following physically-driven events such as upwelling events that inject nutrients into the euphotic zone (Goldman & McGillicuddy 2003). The bloom mechanism in nutrient-rich San Francisco Bay is a release from strong light limitation by other physical processes, including runoff-induced salinity stratification (Cloern 1996) or increased euphotic-zone depth as sediment suspension is damped during weak neap tides (May et al. 2003).

Community studies in San Francisco Bay and in upwelling systems support the empirically-based principle that diatoms respond rapidly to episodic high-light high-nutrient conditions. Surprisingly, there is no consensus explanation of why diatoms best exploit these opportunities for fast population growth. One view is from the bottom up: diatoms divide faster than other taxa, either because they have inherently high growth rates (Smayda 1997), accelerated N assimilation under nitrate-rich conditions (Dugdale & Wilkerson 1992), high growth efficiency at low light (Goldman & McGillicuddy 2003), or because they can utilize bicarbonate during blooms when  $\text{CO}_2$  limits photosynthesis of other algae (Hobson 1988). Other explanations work

from the top down: diatoms succeed because their silica cell wall resists the cracking force of feeding structures such as copepod mandibles (Hamm et al. 2003) and attack by small predatory flagellates or pathogens (Smetacek 1995). Large diatoms can regulate their buoyancy (Waite et al. 1992) to suppress sinking, and this is important in shallow environments such as San Francisco Bay, where most phytoplankton production is consumed by benthic suspension feeders and avoidance of the benthic boundary layer is a key to population survival.

**(3) Pelagic habitats select phytoplankton species on the basis of their form and function:** Hutchinson's paradox came from the premise that phytoplankton species are functional equivalents competing for finite resources in an 'isotropic' fluid medium. However, Margalef (1978) later recognized the ecological significance of variability among species in their form (size, density) and function (motility, behavior) as adaptations to an 'unstable and turbulent environment'. Margalef's Mandala is now a central paradigm of phytoplankton community ecology, expressing the principle that phytoplankton life forms are adaptations to specific pelagic habitat types defined along gradients of turbulence intensity and nutrient concentrations (Cullen et al. 2002). As an alternative to the resource-competition perspective, Margalef (1978) postulated that the 'combination of sedimentation with turbulence' shapes communities as the pelagic varies between extremes of a fertile-turbulent state (promoting diatom growth) and exhausted-stratified state (promoting growth of flagellates and dinoflagellates that migrate vertically to exploit nutrient gradients; Smayda & Reynolds 2001). This framework provides a basis for exploring the diverse patterns of species occurrence in estuaries. One pattern in San Francisco Bay is restricted seasonal occurrence, exemplified by the marine diatoms (Fig. 5A) that dominate spring blooms. A second pattern, exemplified by *Mesodinium rubrum* and some dinoflagellates (Fig. 5B), is nonseasonal population growth in response to short-term events, such as sunny calm weather that establishes an ephemeral thin upper layer within which motile species accumulate (Cloern et al. 1994). *Gyrosigma fasciola* illustrates a different nonseasonal pattern (Fig. 5C) driven by wind events and periodic tidal stresses that suspend benthic forms into the plankton.

Margalef's (1978) conceptual framework also provides a foundation for exploring the diversity of community dynamics among coastal ecosystems. The textbook depiction of phytoplankton seasonality at temperate latitudes is dominance by diatoms in spring and dinoflagellates in summer, but this idealized seasonal succession does not occur in San Francisco Bay or in the Bay of Brest (perennial diatom dominance:



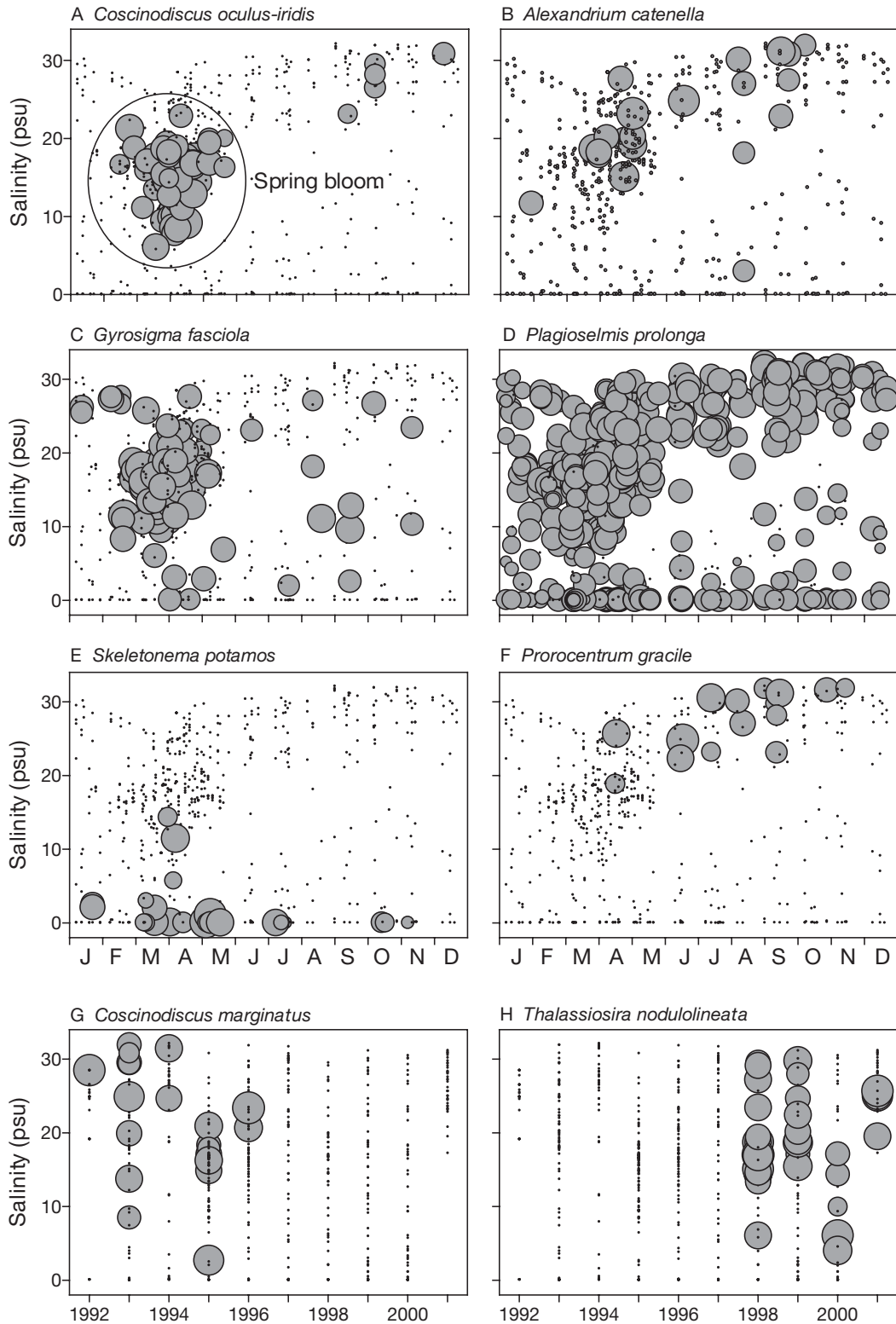


Fig. 5. (A–F) Six different patterns of phytoplankton seasonal occurrence and distribution along the estuarine salinity gradient of San Francisco Bay; size of data points is proportional to  $\log(\text{biomass})$  of individual species in each sample; small dots: samples from which the species was absent. (A) Dominant during spring blooms; (B) episodic occurrences of planktonic species; (C) episodic occurrences of benthic species in plankton; (D) persistent and cosmopolitan distribution; (E) input of freshwater species by river inflow; (F) input of coastal ocean species. (G, H) Changes during the decade of observation, showing coastal species that disappeared after 1996 (G) and appeared after 1997 (H)

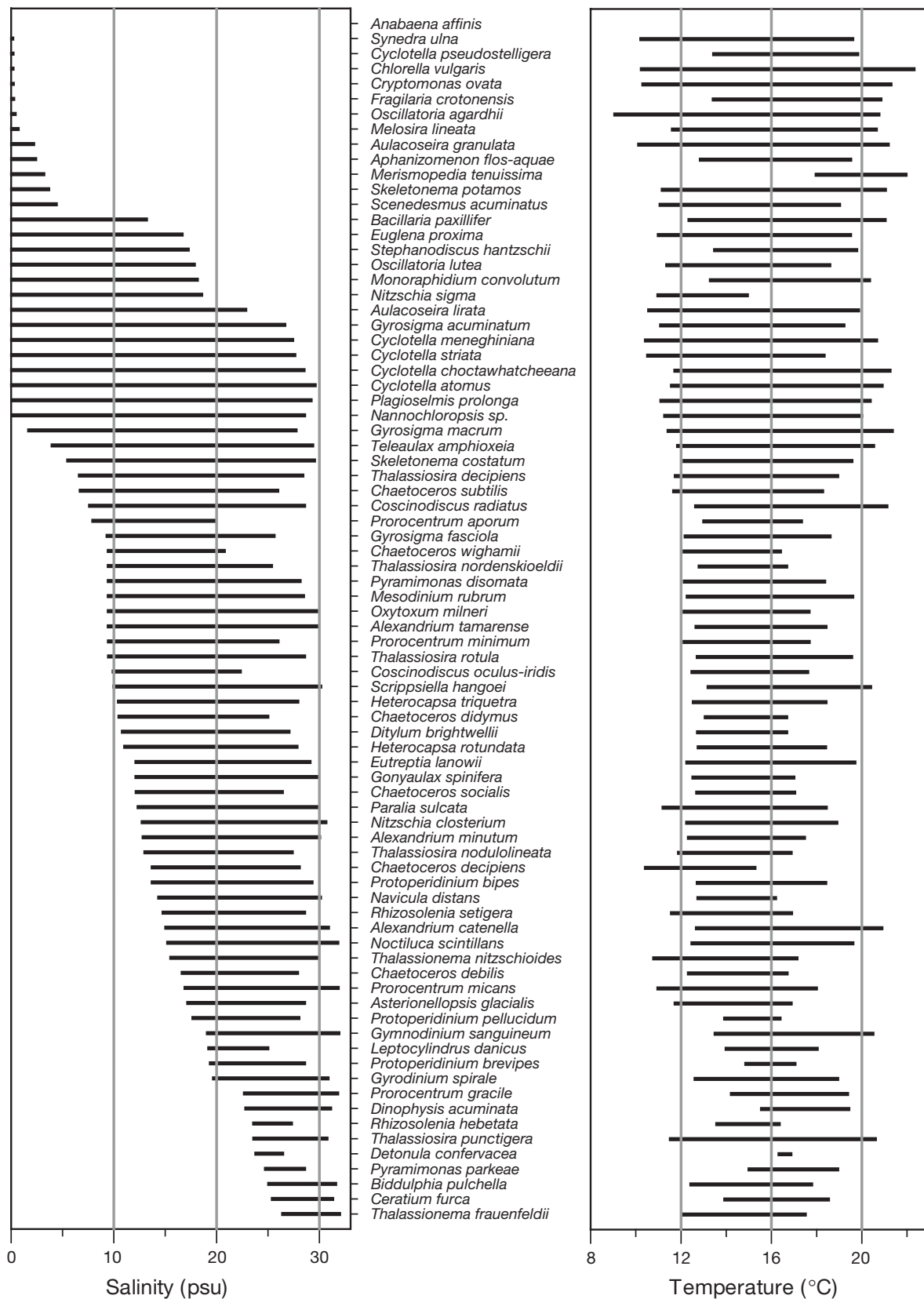


Fig. 6. Salinity and temperature ranges of selected phytoplankton species. Horizontal bars span 10th and 90th percentile salinity and temperature at which each species occurred within 599 samples distributed along salinity gradients of San Francisco Bay (Fig. 2B,C)

Del Amo et al. 1997), Neuse River Estuary (dinoflagellate dominance in winter: Mallin & Paerl 1994), Gulf of Naples (small diatoms in summer: Ribera d'Alcalà et al. 2004), Orbetello Lagoon (cryptophytes in winter and spring: Nuccio et al. 2003), or Norwegian fjords (coccolithophorids in summer: Smayda 1980). Diatoms contribute over 80% to phytoplankton biomass in San Francisco Bay, but dinoflagellates contribute over 85% to biomass in the Patapsco River estuary (Sellner et al. 2001), and biomass is evenly distributed among diatoms, dinoflagellates, cryptophytes, chlorophytes and cyanobacteria in the Neuse River Estuary (Pinckney et al. 1998). Margalef's Mandala suggests the (as yet untested) hypothesis that this large community variability between ecosystems is a consequence of differences in their input of exogenous energy and the persistence of vertical structure in their pelagic habitats.

Margalef's (1978) conceptual framework was built from the principle that specialized life forms have evolved as adaptations to physical habitat variability, but some species are clearly generalists. The picocyanobacteria and some small eukaryotes (*Nannochloropsis* sp., *Teleaulax amphioxeia*, *Plagioselmis prolonga*) are persistent and ubiquitous across large habitat gradients in San Francisco Bay (Fig. 5D), implying resilience to variability in turbulent mixing, optical properties, salinity and temperature. Some marine species (*Thalassiosira frauenfeldii*, *Ceratium furca*, *Pyramimonas parkeae*) are confined to near-coastal domains of San Francisco Bay (Fig. 6) and some freshwater species (*Anabaena affinis*, *Synedra ulna*, *Cryptomonas ovata*) are confined to the tidal river, but many others occur across broad salinity and temperature ranges (Fig. 6). These generalist species are apparently not constrained to occupying fixed niches, so their seasonal occurrences and timing of peak biomass can vary markedly from year to year (Karentz & Smayda 1984). One mode of resilience to environmental variability is the occurrence within morphospecies of genetically distinct strains having variable life histories (French & Hargraves 1986, Montresor et al. 2003), growth rates (Rynearson & Armbrust 2000), and tolerance to salinity and temperature variability (Krawiec 1982).

**(4) Pelagic communities are shaped by species interactions across trophic levels:** The mean doubling time of phytoplankton in San Francisco Bay is only about 4 d (Cloern et al. 1985) but, except during blooms, biomass does not build up (Fig. 2E) because most phytoplankton primary production is consumed at a comparable rate. Many metazoan and protistan consumers are selective in their herbivory, exerting a top-down control on phytoplankton community composition. Based on this principle, Verity & Smetacek (1996) suggested that the traditional emphasis on

resource-driven community regulation has been self-limiting, and they proposed a revised conceptual framework 'that predation and resource availability act through morphologies and life history strategies of organisms to structure pelagic ecosystems'. The calanoid copepod *Acartia* sp. adapts its diet with selectivity in San Francisco Bay for large flagellates and diatoms (*Coscinodiscus* spp., *Thalassiosira* spp.), the chain-forming diatom *Skeletonema costatum*, and dinoflagellates (Rollwagen-Bollens & Penry 2003). The microheterotrophs ingest small forms, with very fast (up to 2 d<sup>-1</sup>) consumption of picocyanobacteria (Murrell & Hollibaugh 1998).

The phytoplankton have evolved a battery of taxon-specific chemical, morphological and behavioral defenses against predation. For example, some dinoflagellates (*Gymnodinium catenatum*, *Dinophysis acuminata*, *Alexandrium* spp.) synthesize metabolites that inhibit feeding and growth of copepods (Carlsson et al. 1995, Teegarden 1999, Calbet et al. 2002). Some algae synthesize multiple compounds which inhibit growth of bacteria, other phytoplankton, protozoan and metazoan grazers (Fistarol et al. 2003) to structure planktonic communities from both the top down and bottom up. At least 20 marine phytoplankton species are infected with host-specific viruses (Zingone et al. 1999), suggesting that pathogens play an important role in regulating phytoplankton biomass and species composition (Short & Suttle 2003). We have just begun to explore the population ecology of algal pathogens and chemically-based species interactions, but these forces of community assembly are just as powerful as resource competition and habitat selection (Zingone & Wyatt 2004). Many of these biological interactions were unknown in Hutchinson's era, so the 1961 conceptual framework was missing key processes now viewed as central regulators of pelagic community structure.

**(5) Phytoplankton species have mixed nutritional modes:** Hutchinson (1961) and his contemporaries knew the phytoplankton as obligate phototrophs competing for a finite number of resources. The presumption of strict phototrophy was shattered by discoveries (e.g. Bird & Kalff 1986, Estep et al. 1986) that some phototrophic flagellates ingest bacteria, and dinoflagellates feed on other algae with 'zipper-like 'mouths' for swallowing food, peduncles or feeding tubes for 'sucking-up' whole prey or their cytoplasmic contents, and feeding veils for encasing and externally digesting large prey' (Coats 2002). Mixotrophic algae are key components of phytoplankton communities including the 2 prominent non-diatom groups in San Francisco Bay: dinoflagellates (mixotrophic species of *Dinophysis*, *Prorocentrum* and *Alexandrium*) and cryptophytes (species of *Plagioselmis*, *Teleaulax*, *Rhodomonas* and *Cryptomonas*).

The discovery of mixotrophy was important because it revealed that phytoplankton can tap the nutrient pools contained in microbial biomass, relaxing the constraint of strict growth regulation by the supply of inorganic nutrients. Bacterial grazing by algal flagellates is a mechanism for acquiring particulate organic P to sustain blooms even at growth-limiting concentrations of dissolved inorganic P (Nygaard & Tobiesen 1993). Although we know very little about the energetics of mixotrophs, their capacity to acquire energy heterotrophically also provides a mechanism to survive in habitats such as turbid estuaries where photosynthesis is strongly light-limited. The ubiquity and persistence of cryptophytes (Fig. 5D) may reflect their ability to ingest bacteria as a heterotrophic supplement to light-limited phototrophy. The discovery of mixotrophy revealed that phytoplankton species are not all functional equivalents occupying one trophic level. Even for the primary producers, species do not 'clearly aggregate into discrete, homogeneous trophic levels' (Polis & Strong 1996).

**(6) Phytoplankton species have variable life histories:** Since Hutchinson's era we have discovered that many algal species have different life forms, including planktonic vegetative and benthic or suspended resting stages (e.g. Dale 2001). Life cycles were not explicitly included in conceptual models of phytoplankton community ecology until Smetacek (1985) postulated that mass sedimentation of bloom diatoms is a life history adaptation to nutrient depletion of surface waters, a survival strategy creating a stock of resting cells to seed population growth when seasonal mixing brings nutrient-rich bottom waters back to the surface. Many neritic species produce benthic resting stages, and the sediments of coastal ecosystems contain a reservoir of diatom spores or resting cells and dinoflagellate cysts that provide a ready inoculum to seed blooms. Production of benthic stages is also a mechanism to retain a species' genome within strongly advective systems such as estuaries, and this retentive function may explain why 92% of the biomass in San Francisco Bay comes from the 2 algal divisions (diatoms and dinoflagellates) in which spore or cyst production is common.

The cues and periodicity of life-form alternation vary among species, providing another mechanism of biogeographic diversity beyond physical-habitat selection. The dinoflagellate *Alexandrium tamarense* produces cysts that require prolonged dormancy before germination, with a 'univoltine' life cycle of 1 annual alternation between pelagic vegetative and benthic resting stages (Montresor et al. 1998). *Scrippsiella trochoidea* has a 'multivoltine' life strategy, producing resting stages that require short periods of dormancy and repeated cycles between life forms within a year. Annual cycles of excystment are regulated by endo-

genous rhythms (*A. tamarense*, Anderson & Keafer 1987), or triggered by exogenous cues. Spore stages of common diatoms in San Francisco Bay (*Chaetoceros socialis*, *C. debilis*, *C. decipiens*, *Thalassiosira nordenskioeldii*, *Rhizosolenia setigera*) germinate only when the photoperiod reaches 13 h (Eilertsen et al. 1995), a mechanism of providing viable inocula to seed spring blooms that is not related to water column stability or nutrient availability.

**(7) Pelagic ecosystems are open:** We now conceive the pelagic as an open system in which immigration and dispersal sustain community diversity. The phytoplankton metapopulation of San Francisco Bay includes all taxa in the linked river–estuary–coastal ocean and pelagic–benthic systems (Table 1). The openness of aquatic ecosystems is central to the diversity paradox because theoretical models show that many species can coexist when immigration is included as a process of community assembly (Hubbell 2001). Many key phytoplankton species in San Francisco Bay are the same taxa that develop blooms in the adjacent coastal upwelling system, suggesting that phytoplankton diversity inside the estuary is influenced by exchanges with the coastal Pacific Ocean. Some dinoflagellates and flagellates (*Ceratium* spp., *Alexandrium catenella*, *Prorocentrum micans*, *P. gracile*, *Dinophysis acuminata*, *Heterosigma akashiwo*) occur only within the high-salinity zone of rapid oceanic exchange (Fig. 5F), suggesting these are allochthonous species produced in coastal waters and transported into the bay by surface currents or tidal dispersion. Allochthonous freshwater taxa, such as *Skeletonema potamos* (Fig. 5E), are delivered to the estuary by pulses of river flow. Phytoplankton communities inside the estuary are influenced by exchanges across a third interface, between the sediments and overlying water. Many diatoms sampled in the plankton are benthic (*Entomoneis paludosa*, *Gyrosigma balticum*, *G. fasciola*, *G. acuminatum*, *Pleurosigma strigosum*, *P. normanii*, *Nitzschia pusilla*, *N. [Cylindrotheca] closterium*, *N. sigma*) or meroplanktonic forms (*Thalassiosira decipiens*, *Cyclotella striata*, *C. meneghiniana*, *Paralia sulcata*, *Actinopterychus senarius*) common in surficial sediments. Many freshwater taxa (*Melosira varians*, *M. moniliformis*, *Bacillaria paxillifer*, *Achnanthes* spp.) are common periphyton components in the tributary rivers, so plankton species richness is augmented by suspension of epipelagic-epiphytic microalgae as an immigration process that was recognized by Hutchinson (1961).

**(8) Communities respond to large-scale climatic periodicity:** In Hutchinson's era we were unaware of large-scale climatic fluctuations such as ENSO events or longer-period climatic cycles such as the Pacific Decadal Oscillation (PDO) and their influence on

pelagic community dynamics. Our perception in that era was that phytoplankton population dynamics follow recurrent patterns of species occurrence each year. Sustained observations and examination of microfossils in the sedimentary record (e.g. Dale 2001) have since revealed that communities and seasonal patterns change, sometimes dramatically, and that these shifts are coherent with annual variability and interdecadal trends of climate change (McGowan et al. 1998). During our decade of observation in San Francisco Bay, some phytoplankton taxa (*Prorocentrum aporum*, *Coscinodiscus marginatus*, *Protoperdinium depressum*, *Eucampia zodiacus*) apparently disappeared after 1996 (Fig. 5G) while others (*Protoperdinium bipes*, *Pseudo-nitzschia delicatissima*, *Scrippsiella trochoidea*, *Thalassiosira nodulolineata*) first appeared, and have occurred yearly, since 1997–1998 (Fig. 5H). The general timing of these changes is coherent with a regime shift in the PDO and large-scale changes in ocean temperature, regional wind patterns, and biological communities across the Pacific basin (Chavez et al. 2003).

Manifestations of this shift included strengthening of equatorward winds and surface currents, increased abundances of cold-water species of copepods and decreased abundances of warm-water species, and altered distributions and abundance of euphausiids in the Eastern Pacific Boundary Current system after 1997–1998 (Swartzman & Hickey 2003). Simultaneous species appearances and disappearances in San Francisco Bay suggest that climate-driven changes in coastal plankton communities can propagate to induce community change within estuaries. Estuarine communities evolve continuously, driven by climatic trends (Chiba & Saino 2002, McQuoid & Nordberg 2003, Zingone & Wyatt 2004), but also global species translocations (Hallegraeff & Bolch 1992) and disturbances such as eutrophication (Anderson et al. 2002).

### Ecological significance of phytoplankton functional diversity

Phytoplankton photosynthesis is the primary energy supply to metazoan food webs of San Francisco Bay (Jassby et al. 1993, Sobczak et al. 2002) and other estuaries. The efficiency of energy transfer from phytoplankton to consumers and ultimate production at upper trophic levels vary with algal species composition: diatom-dominated marine upwelling systems sustain 50 times more fish biomass per unit of phytoplankton biomass than cyanobacteria-dominated lakes (Brett & Müller-Navarra 1997). The nutritional quality of algae varies with its elemental composition and content of highly unsaturated fatty acids (HUFA), par-

ticularly eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). Growth and fecundity of invertebrates are strongly correlated with the HUFA content of their food (Brett & Müller-Navarra 1997), and HUFA-rich diets are essential for development of invertebrate and vertebrate larvae (Olsen 1999). The 17 top ranked species, contributing 89% to phytoplankton biomass in San Francisco Bay, comprise 12 diatoms, 2 dinoflagellates, 2 cryptophytes, and *Mesodinium rubrum*. Marine dinoflagellates are rich in DHA, diatoms are rich in EPA (Olsen 1999), and cryptophytes have high contents of both (Ravet et al. 2003), so the phytoplankton in San Francisco Bay are of high nutritional quality. This suggests the hypothesis that trophic efficiency leading to production at upper trophic levels is also high. Estuaries are rearing habitats for shrimp, crabs, bivalves, demersal and pelagic fishes, and this nursery function includes algal supply of both energy and essential biochemicals. The high nutritional quality of diatoms and dinoflagellates may contribute to the generally higher efficiency of fish production in estuarine–marine regions compared to freshwater lakes (Nixon 1988).

This traditional view of efficient diatom-based food webs has been challenged since discoveries that copepods often select other food items (Kleppel 1993) and have lower fecundity when fed diatom versus non-diatom diets. This 'diatom–copepod paradox' (Ban et al. 1997) is the conflicting high nutritional quality yet potential toxicity of diatoms to consumers. Some diatoms, including key species in San Francisco Bay (*Thalassiosira rotula*, *Skeletonema costatum*, *Chaetoceros debilis*, *Ditylum brightwellii*) synthesize aldehydes that block mitosis and arrest development of invertebrate eggs (D'Ippolito et al. 2002). Although there is uncertainty about the impairment of consumers in natural environments (Colin & Dam 2002), the prominence of these diatoms in San Francisco Bay suggests that secondary production might be disrupted by episodic blooms of key species that synthesize cytotoxic biochemicals.

Pathways and efficiencies of energy transfer within pelagic food webs vary also with phytoplankton cell size and nutritional mode. Size is important because many metazoan consumers, such as calanoid copepods, cannot capture small particles, including the nutritionally-rich nanoflagellates (Fenchel 1988). We binned key phytoplankton species of San Francisco Bay into 2 size classes (using 15  $\mu\text{m}$  as the criterion separating small and large algae; Rollwagen Bollens & Penry 2003), and 3 nutritional modes (Fig. 7) distinguishing strict phototrophs and heterotrophic dinoflagellates from mixotrophs capable of heterotrophic nutrition through osmotrophy (*Dinophysis* spp., Prymnesiophytes) and ingestion of bacterial-sized particles

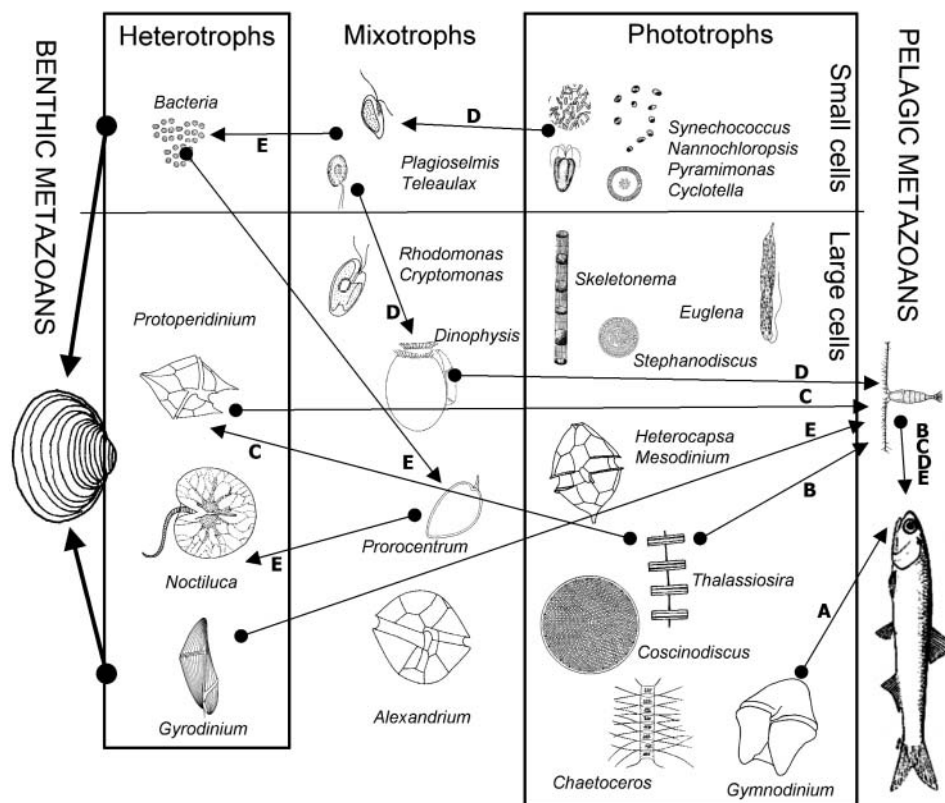


Fig. 7. Phytoplankton classification by size (small cells <15 μm) and nutritional mode that influence pathways through which energy and essential biochemicals are supplied to benthic metazoans (e.g. bivalve mollusks) and pelagic metazoans (e.g. copepods and anchovies). Trophic Pathway A is an efficient direct link from large-cell phototrophs to larval fishes. Other pathways route energy through mesozooplankton: (B) directly from large-cell phototrophs, (C) from heterotrophic algae feeding on large-cell phototrophs, or (D) from mixotrophs or (E) microheterotrophs deriving energy fixed by small-cell phototrophs and routed through the microbial loop. Some images redrawn from Tomas (1993, 1996)

(cryptophytes, *Heterosigma* spp., *Prorocentrum* spp.) or small phototrophs (*Gymnodinium* spp., *Oxyrrhis* spp.).

Taxa within each bin fulfill distinct functions, including a diverse array of feeding linkages that cumulatively set the energy supply to metazoans. We illustrate 5 trophic pathways (Fig. 7) leading from phytoplankton primary production to production of northern anchovy *Engraulis mordax*, the most abundant fish species in San Francisco Bay. Anchovy larvae feed on large dinoflagellates including *Gymnodinium* (*Akashiwo sanguineum*), so they can function as primary consumers (Trophic Level 2) when they utilize this pathway exclusively (Fig. 7A). Other pathways lead to anchovy consumption of mesozooplankton such as copepods, and the most direct is through copepod predation on phototrophs, with selection for the preferred species *Mesodinium rubrum*, flagellates, *Skeletonema costatum*, *Thalassiosira* spp., and *Coscinodiscus* spp. (Rollwagen-Bollens & Penry 2003). This pathway (Fig. 7B) places anchovies at Trophic Level 3, and it dominates during the spring bloom when large-cell primary production is high enough to support

maximum rates of copepod feeding and reproduction. Heterotrophic dinoflagellates such as *Protoperidinium* spp. compete with copepods for large algal cells (Olli & Heiskanen 1999), and themselves are consumed by copepods. The heterotrophic dinoflagellates introduce an additional trophic linkage between phototrophs and mesozooplankton (Fig. 7C), moving anchovies to Trophic Level 4. Although the energy contained in small algal cells is not directly accessible to adult copepods, the mixotrophic algae function as intermediary consumers to repackage a fraction of this energy into accessible forms. The most direct pathway (Fig. 7D) links picocyanobacteria (*Synechococcus* spp.) to small mixotrophs (*Plagioselmis* spp., *Teleaulax* spp.), then larger mixotrophs (*Gymnodinium* spp., *Dinophysis* spp.) and copepods, placing anchovies at Trophic Level 5. Longer pathways (Fig. 7E) to copepods, from bacteria to mixotrophs such as *Prorocentrum* spp. and then to heterotrophic dinoflagellates such as *Polykrikos* spp. and *Noctiluca* spp., place anchovies at Trophic Level 6. Assuming that the growth efficiency of protists is 0.25 and that of metazoans is 0.1, potential anchovy

production can range from 10% of primary production when based solely on consumption of phototrophic dinoflagellates to only 0.016% of primary production when based on the longest pathways (Fig. 7E). Neither of these idealized pathways operates to the exclusion of others, but this comparison illustrates how phytoplankton size and nutritional mode influence the ecological efficiency of food webs supporting pelagic fish production.

Phytoplankton size structure also influences energy allocation between the competing benthic and pelagic food webs because of differences in size-selective feeding between benthic suspension feeders (e.g. bivalve mollusks) and crustacean zooplankton (e.g. calanoid copepods). Ciliary feeding provides bivalves access to a broad size spectrum of food particles, including the bacterial-sized picoplankton and smallest eukaryotes (Wetz et al. 2002) that are inaccessible to many pelagic crustaceans. Trophic linkages from small-cell primary producers (species of *Synechococcus*, *Nannochloropsis*, *Pyramimonas*, *Plagioselmis*, *Cyclotella*) to benthic metazoans are direct and efficient because no intermediary steps of transformation (and associated respiratory loss) are required. The stable biomass of picoplankton and small cryptophytes provides a ubiquitous food resource to benthic invertebrates, whereas the size-selective copepods are more dependent upon the episodic bursts of large-cell production during blooms. Copepods utilize trophic pathways that are less efficient and less reliable than those of bivalves, and this distinction partly explains why benthic metabolism often exceeds pelagic metabolism in shallow marine systems (Caffrey et al. 1998), benthic macrofaunal biomass exceeds mesozooplankton biomass (Baretta et al. 1988), and alien bivalves successfully compete with zooplankton for the phytoplankton food resource, leading to dramatic declines of zooplankton abundance following invasions by alien bivalves (Orsi & Mecum 1996).

### Resolution of Hutchinson's paradox and a remaining big challenge

The plankton diversity problem was originally conceived as one of low dimensionality, whereby communities were presumably assembled by competition operating along a few resource gradients. Now we conceive the problem as hyperdimensional, whereby communities are assembled by selective forces operating on variation in algal size, motility, behavior, life cycles, biochemical specializations, nutritional mode, chemical and physiological tolerances, and dispersal processes. Diversity is promoted by variability along each of these dimensions. Four decades of discovery

and conceptual-model revisions have resulted in a more complete and mechanistic understanding of why phytoplankton diversity exceeds that predicted from equilibrium resource-competition theory.

Resolution of Hutchinson's (1961) plankton diversity paradox has come from progress in understanding phytoplankton community assembly at the level of form, function and growth habitat: small versus large, motile versus nonmotile, allochthonous versus autochthonous, benthic versus pelagic taxa. This has not yielded comparable advances in our knowledge of community assembly at the level of species. Marine ecologists understand, at least generally, why diatoms dominate in turbulent nutrient-rich habitats, but not why *Thalassiosira rotula* is the Rank 1 species in San Francisco Bay or why toxic species are present but do not form harmful blooms in this estuary, as they do in others. The rules of phytoplankton community assembly at the species level remain elusive, with 1 general principle, that 'the ultimate influences of species composition are precedent and stochasticity' (Reynolds et al. 2000). The underlying processes will not be revealed until we fill in details of the matrix of key species and their repertoires of attributes on which the selective processes of community assembly operate, including intraspecies genetic diversity (Zingone & Wyatt 2004). We know surprisingly little about the life cycles, behavior, energetics, biochemical pathways, resource requirements, susceptibility to pathogens, genetic variability and even growth rates of many key species such as the ubiquitous and ecologically important cryptophytes. Our knowledge base is therefore insufficient for constructing reliable numerical models of phytoplankton population dynamics at the species level, in spite of our recognition that the functions provided by the phytoplankton vary among species (Fig. 7).

Resolution of the species assembly puzzle demands investment in a mode of scientific investigation grounded in autecology, organism interactions and life history that is perceived as unfundable or outmoded (Dale 2001, Smetacek et al. 2002). Until this investment is made, our capacity to understand the mechanisms of phytoplankton species dynamics, their ecological and biogeochemical significance, and their variable patterns between ecosystems will remain stifled (Verity & Smetacek 1996, Reynolds 1998). Given the imperative of forecasting ecological responses across the fast-changing landscapes of the Earth system (Clark et al. 2001), species-level studies are required to build the foundation for constructing models of pelagic community responses under plausible scenarios of environmental change through nutrient enrichment, introductions of alien species, hydrologic manipulations and global warming. Resolution of Hutchinson's paradox is a source of intellectual satisfaction derived from

progress in identifying the processes that assemble communities at one level. The remaining big challenge is to understand how these processes interact to assemble phytoplankton communities at the next, more formidable, level of species.

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