

10 Harmful Algal Bloom Dynamics in Relation to Physical Processes

F.G. FIGUEIRAS, G.C. PITCHER, and M. ESTRADA

10.1 Introduction

The term harmful algal bloom (HAB) has been applied to a diverse range of phytoplankton to which harmful impacts have been attributed. These algae belong to a wide variety of phylogenetic groups. The dinoflagellates, raphidophytes, and prymnesiophytes have historically been considered the primary cause of HABs, but other groups of phytoplankton, such as the diatoms and cyanobacteria now also include taxa known to be harmful.

HAB dynamics are influenced at all spatial-temporal scales relevant to phytoplankton physiology, ecology, and distribution; from the level of short-lived sub-cellular physiological processes to global biogeographical ranges and long-term fluctuations of natural populations (Donaghay and Osborn 1997; Zingone and Wyatt 2005; Franks 2006). Harmful algal blooms should not be considered marginal biological phenomena. The view that HABs are irregular, unpredictable events is misleading, when in fact many harmful species constitute normal components of the seasonal succession of phytoplankton driven by exogenous forces, which contribute to the establishment of habitat templates favoring one or another phylogenetic or functional groups.

The upper ocean is physically forced by air–sea interactions, land and rivers, and the ocean interior. Winds force various physical processes, which are not mutually independent, such as waves, currents and turbulence. Coherent flow structures and convection further complicate upper ocean dynamics (Yamazaki et al. 2002). Hence, the upper ocean is the site of a myriad of interacting dynamic physical processes, all of which influence the functioning and distribution of organisms both directly and indirectly. Direct effects include those of turbulence in altering algal growth rates (Berdalet 1992; Juhl and Latz 2002; Sullivan et al. 2003), cell shape (Zirbel et al. 2000), and the transport of substances in and out of cells (Karp-Boss et al. 1996). The establishment of aggregations required for sexual exchange or the ability of grazers to capture

cells is also directly influenced by turbulence in determining encounter rates and perceptive abilities (Yamazaki et al. 2002). Indirect physical effects include the influence of mixing patterns on the distribution of temperature and nutrients, and the transport of phytoplankton in or out of the euphotic zone.

This chapter focuses on the indirect effects of water motion and turbulence on HAB development, as mediated through transport, and provides examples of various ecosystem types in which these processes are operative.

10.2 Physical Constraints: From Diffusion to Advection

Phytoplankton inhabits a heterogeneous environment in which diffusion ($K_{x,y,z}$) and advection ($V_{x,y,z}$) are the main physical processes influencing population development. In this environment, the rate of change of any harmful algal population at a particular location (dN/dt) can be defined as a function of these two physical fluxes and growth (μ):

$$dN/dt = K_x \partial^2 N / \partial x^2 + K_y \partial^2 N / \partial y^2 + K_z \partial^2 N / \partial z^2 - V_x \partial N / \partial x - V_y \partial N / \partial y - V_z \partial N / \partial z + \mu N \quad (10.1)$$

Diffusion tends to reduce the spatial gradients of a population by mixing across gradients. Mixing tends to decrease the density of local population maxima, and increase local population minima by mixing from regions of high concentration to low. While vertical mixing tends to be many orders of magnitude weaker than horizontal mixing, the strong vertical gradients of many physical and chemical properties make vertical mixing of fundamental importance to biological phenomena.

Advection is driven by physical velocities, which move spatial gradients of a population in x , y and z directions. The importance of these terms depends on the relative strengths of these velocities and of the spatial gradients of the populations. Swimming can be formulated as a term for vertical advection (Margalef 1978) that may counter physically driven losses. Organism motility and its behavioral control (Kamykowski et al. 1998; Karp-Boss et al. 2000; Sullivan et al. 2003) interact with water circulation patterns and play a key role in favoring retention (Seliger et al. 1970; Anderson and Stolzenbach 1985) or accumulation (Tyler and Seliger 1981; Fraga et al. 1988; Figueiras et al. 1995) of motile phytoplankton. Swimming alters population gradients and leads to surface or subsurface accumulations of phytoplankton, especially in environments with downward water motions such as negative estuaries, convergent fronts or Langmuir circulation cells (Holligan 1979; Kamykowski 1981). The superior swimming ability of chain-forming dinoflagellates, like *Gymnodinium catenatum* or *Alexandrium catenella* (Fraga et al. 1989) or of ciliates

such as *Mesodinium rubrum*, enables them to balance relatively strong dispersing currents and to form blooms in high-energy frontal zones.

10.3 Life-Forms

Determination of the particular characteristics and adaptations that enable a harmful species to bloom is complicated by the considerable physiological and phylogenetic variety presented by these microalgae. Physiological factors increasing the net-growth-rate parameter (μ), such as a rapid intrinsic division rate or allelopathic defenses against predation, are important in determining the bloom-forming capability of some species. However, these factors are in many instances overridden by the ecological response to hydrodynamic forcing. Margalef (1978) considered the available external energy, controlling water movement and nutrient supply, the key factor determining the selection of phytoplankton species. Populations selected under recurrent patterns of environmental conditions tend to share sets of *characteristics*, or *adaptation syndromes*, which provide a basis for the classification of phytoplankton life-forms, as depicted in the *phytoplankton mandala* of Margalef (Fig. 10.1a), in which major taxonomic groupings are presented as *proxies* for phytoplankton life-forms. Diatoms tend to dominate in high-nutrient, relatively high-turbulence conditions, while (*flat*) dinoflagellates are better adapted to survival

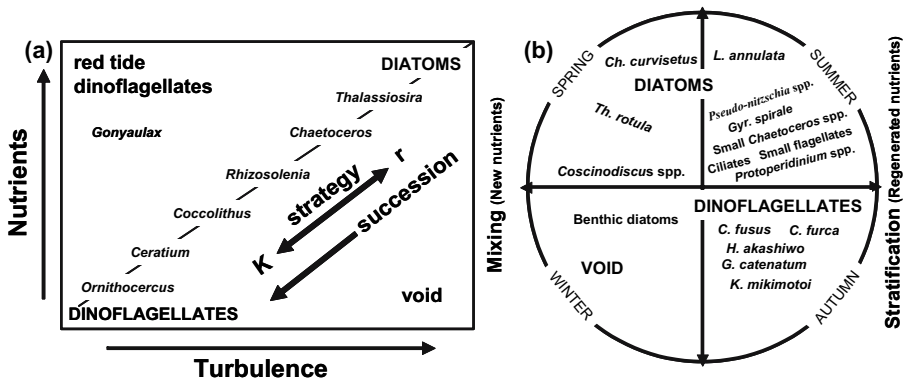


Fig. 10.1. Phytoplankton succession and life-forms in an ecological space defined by turbulence and nutrient concentration, as depicted by the mandala of Margalef (a) and annual cycle of phytoplankton abundance in The Rías Baixas of Galicia (b) (see Fig. 10.4a for location) according to a mixing-stratification (new vs. regenerated nutrients) gradient. HABs are found to correspond to conditions of high nutrients and low turbulence. (a) Reprinted from *Oceanologica Acta*, volume 1, R. Margalef, pages 493–510, Copyright (1978), with permission from Elsevier. (b) Redrawn and simplified from Figueiras and Niell (1987)

under low-nutrient, low-turbulence conditions. Red-tide-forming (*rounded*) dinoflagellates are shown to be associated with high nutrient, low turbulence conditions. In general, given adequate nutrient supply, diatoms tend to have faster growth rates than other phytoplankton groups (Brand and Guillard 1981), but some level of upward advection or turbulent mixing may be required to maintain their populations in sufficiently illuminated conditions (Huisman et al. 2002). In contrast, motility may represent an important asset in a stratified environment by regulating position in the water column thereby determining nutrient uptake and the light environment. The association of red-tide-forming dinoflagellates with low turbulence may result primarily from reduced physical dispersion, thereby permitting the accumulation of algal biomass (see Eq. 10.1), rather than from any direct effects of turbulence on dinoflagellates. The mandala represented a conceptual model stressing the importance of hydrodynamic forcing relative to physiological responses to light or nutrient concentration (Margalef 1978; Margalef et al. 1979) and was never meant to provide a detailed prescription of taxonomic ordination. Its basic application (Fig. 10.1b) has been shown in numerous studies (Bowman et al. 1981; Jones and Gowen 1990; Figueiras and Ríos 1993; Vila and Masó 2005).

The life-form ordination of the *mandala*, which has been expanded by other authors (Cullen and MacIntyre 1998; Smayda and Reynolds 2001), emphasizes the importance of morphotypic properties, such as size and shape, and behavioral features related to the control of buoyancy or motility (see Sect. 10.2). Life-cycle strategies are also important in the context of the physical environment in that cyst or temporary cyst formation may be utilized to avoid dispersion (Garcés et al. 1999) and to reseed the water column (Anderson et al. 2005).

10.4 Algal Communities

The composition of microalgal communities reflects life-form selection modulated by species-specific features. Therefore, species assemblages tend to share similar functional characteristics in response to the ecological history of the body of water in which they are found. Although the dominance of a particular species within an available biodiversity pool may be reduced to a statistical probability, experience shows that phytoplankton communities can be characterized as assemblages of co-occurring species that show relatively persistent temporal and spatial patterns in composition (Blasco et al. 1981; Venrick 1999). Therefore, in spite of their occasional conspicuous dominance, harmful species do not occur in isolation, but rather as a group. Identification of assemblages incorporating HAB species, and their association with particular physical-chemical properties may therefore provide a predictive capabil-

ity. For example, the toxic dinoflagellate *Gymnodinium catenatum* was observed in the Iberian upwelling system as a regular component of an assemblage of dinoflagellates including *Prorocentrum triestinum*, *P. micans*, *Ceratium fusus* and *Dinophysis acuta*. The detection of this assemblage in the rías could be used to warn of the likely appearance of *G. catenatum* (Figueiras et al. 1994; Fermín et al. 1996).

10.5 Retention and Transport

Ecosystems are often classified according to the relative importance of one or another physical process. These may include systems categorized by retention or reduced exchange, and others categorized by advective processes.

10.5.1 Retention-Reduced Exchange

Pycnoclines (Pingree et al. 1975; Nielsen et al. 1990; Kononen et al. 2003), fronts (Pingree et al. 1975; Pitcher and Boyd 1996; Pitcher et al. 1998) and cyclonic eddies (Trainer et al. 2002) tend to reduce exchange with surrounding waters, thereby favoring the accumulation of phytoplankton, which can be enhanced by decreased sinking speed or increased swimming capacity. Within pycnoclines, harmful algae are frequently found in thin layers (Bjørsen and Nielsen 1991; Gentien et al. 1995; Rines et al. 2002). The mechanisms of formation of these layers, which may vary substantially in thickness, spatial extent and duration (Dekshenieks et al. 2001), remain unclear. They may result primarily from physical processes, such as the interaction between vertical shear gradients and the horizontal advection of phytoplankton patches (Franks 1995), or they may require a particular swimming-sinking behavior (Sullivan et al. 2003; Gallager et al. 2004).

Retention and/or reduced exchange are often considered to favor HAB generation in small reservoirs or embayments. Blooms of *Pyrodinium bahamense* in Oyster Bay, Jamaica (Seliger et al. 1970), and of *Alexandrium ostenfeldii* and *Heterocapsa triquetra* in Salt Pond, Massachusetts, USA (Anderson and Stolzenbach 1985) are formed by avoiding water exchange. These populations are able to perform vertical migrations in synchrony with the tides, thereby avoiding tidal flushing. Reduced dispersion is also a requisite for blooms of the nitrogen-fixing and floating cyanobacteria *Aphanizomenon flos-aquae* and *Nodularia spumigena* in the Baltic Sea, which develop during calm weather conditions after the spring bloom when the water column is stratified and surface waters are almost exhausted of inorganic nitrogen (Sellner 1997). Similar effects can occur when diffusion from a water body is hindered by man-made structures or hydrographical features

such as fronts. These considerations, combined with nutrient enrichment or eutrophication owing to land runoff, explain the frequent development of HABs in enclosed or semi-enclosed coastal systems.

The influence of confinement in the development of HAB events was examined in a series of eight harbors distributed along the Catalan coast (NW Mediterranean, Fig. 10.2a, Vila and Masó 2005). These harbors were selected to include anthropogenically impacted areas and a range of harbor sizes. From a total of 171 taxa identified over an annual cycle, 27 were potentially harmful. These included *Alexandrium minutum*, *A. catenella*, several *Dinophysis* species and *Karlodinium* sp. Based on a multivariate analysis, the authors could distinguish four clusters (Fig. 10.2b) that could be assigned to four different functional groups: bloom-forming dinoflagellates, winter diatoms, summer-autumn diatoms and a group including both large dinoflagellates and elongated diatoms. The bloom-forming dinoflagellates included rounded species like *A. minutum*, *Gyrodinium impudicum*, *Prorocentrum triestinum* and *Scrippsiella* spp., which could be considered as *r*-strategists. This group was most abundant in large harbors during the summer. The group comprising large dinoflagellates and elongated diatoms included dinoflagellates such as *Ceratium* spp., with a high surface-to-volume ratio, and the diatom species *Proboscia alata* and *Rhizosolenia* cf. *imbricata*. The diatom groups were named according to their seasonal dominance; namely winter and summer-autumn diatoms. Blooms were typically attributed to the bloom-forming dinoflagellates and to the winter diatoms, while potentially toxic taxa could be found in any one of the four clusters. The study also showed that dinoflagel-

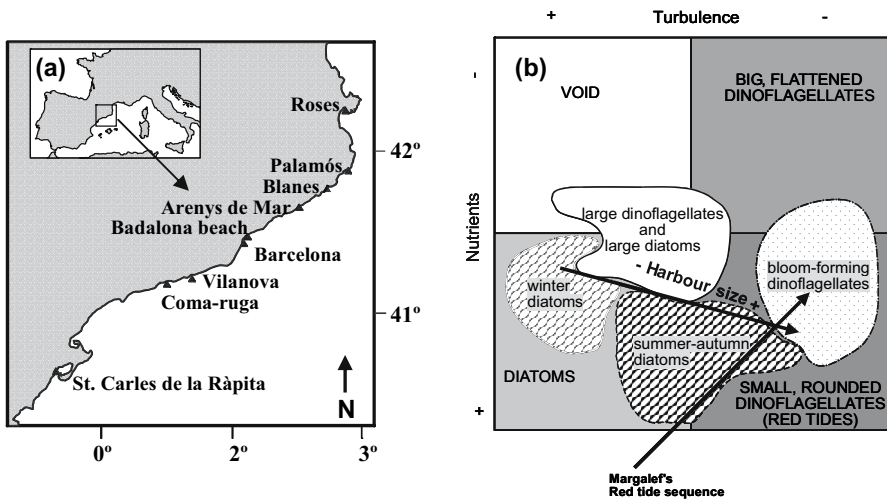


Fig. 10.2. The study of HABs in eight harbors along the Catalan coast (a), including a schematic representation of the four functional phytoplankton groups in the framework of Margalef's mandala rotated through 180° (b) (from Vila and Masó 2005)

lates were more abundant in large harbors ($>15 \text{ km}^2$), and bloom-forming dinoflagellates were less represented in small harbors. The authors considered these variations in the abundance of dinoflagellates to be a function of longer water residence times in larger harbors, which present lower ratios between mouth area and contained water volume than smaller harbors.

10.5.2 Transport

Across-shelf and alongshore currents are known to play a key role in HAB dynamics in coastal waters. Coastal blooms may result from the onshore advection of blooms generated in offshore regions (Pitcher and Boyd 1996; Pitcher et al. 1998; Raine and McMahan 1998; Trainer et al. 2002; Anderson et al. 2005). In other cases, onshore currents interact with coastal morphology and bathymetry to trap dinoflagellate populations in downwelling fronts, where the downward velocity of the water is countered by the ability of dinoflagellates to swim (Fraga et al. 1989; Figueiras et al. 1995). Alongshore currents significantly contribute to the extension of HABs along the coast. Blooms may be transported hundreds of kilometers from their origins by buoyancy currents associated with river outflows (Franks and Anderson 1992) or by surface poleward coastal currents in upwelling systems (Pitcher and Boyd 1996). In other cases, onshore and along-shore currents frequently combine to first accumulate blooms in the coastal region (Pitcher and Boyd 1996; Pitcher et al. 1998; Trainer et al. 2002; Anderson et al. 2005), before transporting them alongshore (Franks and Anderson 1992; Anderson et al. 2005).

Coastal upwelling systems provide an example in which both across-shelf and alongshore currents and retention processes interact to generate HABs. Under upwelling conditions, the general shelf circulation pattern consists of a surface alongshore equatorward current countered by a poleward undercurrent. Ekman transport provides an across-shelf component to the flow with an offshore stream at the surface and compensating onshore flow in deeper layers. The situation is reversed during downwelling, when a surface poleward current is established over the shelf and forces the onshore flow of surface waters. Consequently, the coastal impacts of harmful blooms in upwelling systems coincide with the relaxation phase of upwelling, whereby populations developing offshore during the active phase of upwelling are advected to coastal sites by across-shelf currents and transported alongshore by poleward counter currents. These currents are among the most prominent physical features of coastal upwelling systems and are considered key mechanisms for the initiation of late summer-autumn coastal blooms in several upwelling systems (Fraga et al. 1988; Figueiras et al. 1994; Pitcher and Boyd 1996; Trainer et al. 2002).

Coastline features, such as capes and embayments, particular topographic features of the slope and continental shelf, the presence of buoyant freshwater

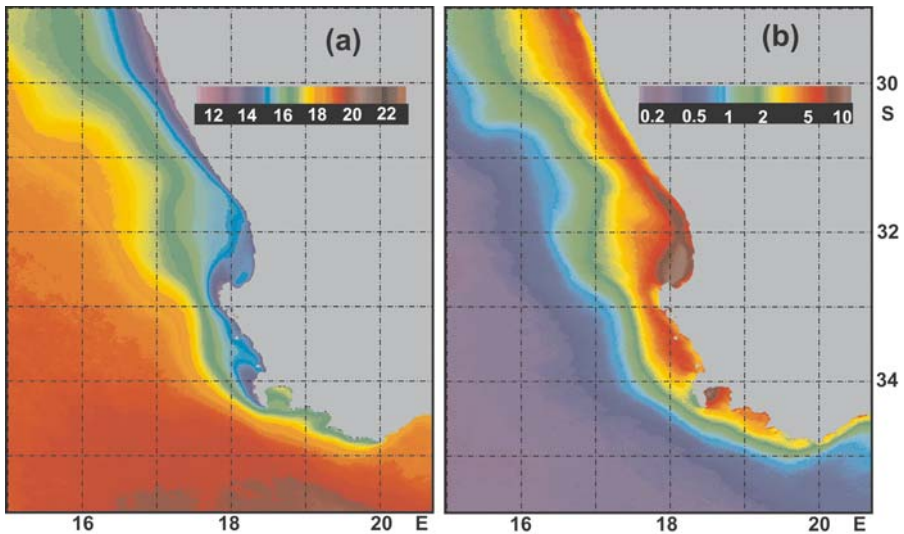


Fig. 10.3. A 5-year (July 1998–June 2003) composite of SST (a) and chlorophyll (b) derived from daily high-resolution (1 km) NOAA AVHRR and SeaWiFS ocean color data. The role of shelf bathymetry and local topography in influencing the upwelling processes and the distribution of phytoplankton biomass is demonstrated (reprinted from Pitcher and Weeks (2006) with permission from Elsevier)

plumes and the dynamics of oceanic margins interact with wind forcing to generate instabilities in flow that alter the general circulation patterns of upwelling systems at various spatial scales. Alongshore and across-shelf flows are modified, resulting in the amplification and/or reduction of upwelling-downwelling processes (Fig. 10.3a). These coastline discontinuities result in considerable alongshore variability and give rise to areas of convergence or retention, which may favor the development of high biomass blooms (Fig. 10.3b). These areas may also function as sedimentary basins accumulating benthic cysts of HAB species that will later function as bloom inocula.

Interaction between coastline features and across-shelf currents also occur in the Galician Rías Baixas (Fig. 10.4a), comprising four bays located on the northern limit of the Iberian upwelling system. Here HABs dominated by dinoflagellates usually occur during the seasonal transitions in upwelling-downwelling. These bays, which have an almost perpendicular orientation to the coast, act to amplify upwelling and downwelling signals and the exchange between the rías and shelf. Thus, during upwelling, the circulation inside the rías consists of an outflow of surface waters and a compensating inflow of coastal bottom water (Fig. 10.4b). During these upwelling events, phytoplankton composition is characterized by the dominance of diatoms inside the rías and a higher incidence of dinoflagellates on the shelf (Tilstone et al. 1994). However, during downwelling conditions, circulation reverses and coastal

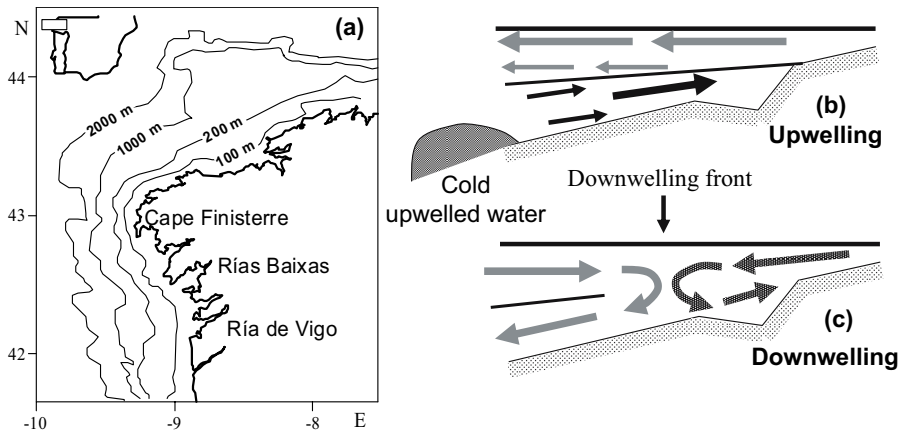


Fig. 10.4. The location of the four Rías Baixas of Galicia on the NW of the Iberian Peninsula (a) and a schematic representation of the circulation within the rías during (b) upwelling and downwelling (c)

surface water enters the rías to form a downwelling front with inner waters of higher continental influence (Fig. 10.4 c). Under these conditions, dinoflagellates are advected from the shelf into the interiors of the rías, where they accumulate in the downwelling front (Fraga et al. 1988; Figueiras et al. 1995; Fermín et al. 1996). This accumulation takes place due to the vertical swimming ability of dinoflagellates which allows them to remain in the water column (Fraga et al. 1989), while diatoms are unable to counteract the downward velocity and are removed from the surface waters.

Bloom transport is also an essential feature of HAB dynamics in the Gulf of Mexico. Blooms of *Karenia brevis*, which are usually initiated offshore, in thermal fronts on the western edge of the Loop Current during upwelling, can be advected towards the coast during periods of wind relaxation. Transport along the Gulf coast of Florida occurs in association with the northward intrusion of the Loop Current. Although *K. brevis* blooms are usually constrained to the west coast of Florida due to the restriction imposed by cyclonic gyres that reduce exchange at both extremes, the blooms are occasionally advected onto the Atlantic side of the Florida coast by the Gulf Stream when the Tortugas gyre debilitates (Tester and Steidinger 1997).

References

- Anderson DM, Stolzenbach KD (1985) Selective retention of two dinoflagellates in a well-mixed estuarine embayment: the importance of diel vertical migration and surface avoidance. *Mar Ecol Prog Ser* 25:39–50
- Anderson DM, Keafer BA, Geyer WR, Signell RP, Loder TC (2005) Toxic *Alexandrium* blooms in the western Gulf of Maine: the plume advection hypothesis revisited. *Limnol Oceanogr* 50:328–345
- Berdalet E (1992) Effects of turbulence on the marine dinoflagellate *Gymnodinium nelsonii*. *J Phycol* 28:267–272
- Bjørnsen PK, Nielsen TG (1991) Decimeter scale heterogeneity in the plankton during a pycnocline bloom of *Gyrodinium aureolum*. *Mar Ecol Prog Ser* 73:263–267
- Blasco D, Estrada M, Jones JH (1981) Short-time variability of phytoplankton populations in upwelling regions. The example of northwest Africa. In: Richards FA (ed) Coastal upwelling. Am Geophys Union, Washington, DC, pp 339–347
- Bowman MJ, Esaias WE, Schnitzer MB (1981) Tidal stirring and distribution of phytoplankton in Long Island and Block Island Sounds. *J Mar Res* 39:587–603
- Brand LE, Guillard RRL (1981) The effects of continuous light and light intensity on the reproduction rates of twenty-two species of marine phytoplankton. *J Exp Mar Biol Ecol* 50:119–132
- Cullen JJ, MacIntyre JG (1998) Behavior, physiology and the niche of depth-regulating phytoplankton. In: Anderson DM, Cembella AD, Hallegraeff GM (eds) Physiological ecology of harmful algal blooms. NATO ASI Series 41. Springer, Berlin Heidelberg New York, pp 559–579
- Deksheniekes MM, Donaghay PL, Sullivan JM, Rines JEB, Osborn TR, Twardowski MS (2001) Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes. *Mar Ecol Prog Ser* 223:61–71
- Donaghay PL, Osborn TR (1997) Toward a theory of biological-physical control of harmful algal bloom dynamics and impacts. *Limnol Oceanogr* 42:1283–1296
- Fermín EG, Figueiras FG, Arbones B, Villarino ML (1996) Short-time scale development of a *Gymnodinium catenatum* population in the Ría de Vigo (NW Spain). *J Phycol* 32:212–221
- Figueiras FG, Niell FX (1987) Composición del fitoplancton en la ría de Pontevedra, NO de España. *Inv Pesq* 51:371–409
- Figueiras FG, Ríos AF (1993) Phytoplankton succession, red tides, and the hydrographic regime in the Rías Bajas of Galicia. In: Smayda TJ, Shimizu Y (eds) Toxic phytoplankton blooms in the sea. Elsevier, Amsterdam, pp 239–244
- Figueiras FG, Jones KJ, Mosquera AM, Álvarez-Salgado XA, Edwards A, MacDougall N (1994) Red tide assemblage formation in an estuarine upwelling ecosystem: Ría de Vigo. *J Plankton Res* 16:857–878
- Figueiras FG, Wyatt T, Álvarez-Salgado XA, Jenkinson I (1995) Advection, diffusion, and patch development of red tide organisms in the Rías Baixas In: Lassus P, Arzul G, Le Denn EE, Gentien P, Marcaillou C (eds) Harmful marine algal blooms. Lavoisier Intercept, Paris, pp 579–584
- Fraga S, Anderson DM, Bravo I, Reguera B, Steidinger KA, Yentsch CM (1988) Influence of upwelling relaxation on dinoflagellates and shellfish toxicity in Ría de Vigo, Spain. *Est Coast Shelf Sci* 27:349–361
- Fraga S, Gallager SM, Anderson DM (1989) Chain-forming dinoflagellates: an adaptation to red tides. In: Okaichi T, Anderson DM, Nemoto T (eds) Red tides: biology, environmental science and toxicology. Elsevier, New York, pp 281–284
- Franks PJS (1995) Thin layers of phytoplankton: a model of formation by near-inertial wave shear. *Deep Sea Res I* 42:75–91

- Franks PJS (2006) Physics and physical modeling of harmful algal blooms. In: Babin M, Roesler CS, Cullen JJ (eds) Real-time coastal observing systems for ecosystem dynamics and harmful algal blooms. UNESCO, Paris (in press)
- Franks PJS, Anderson DM (1992) Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarensis* in the Gulf of Maine. *Mar Biol* 112:153–164
- Gallager SM, Yamazaki H, Davis CS (2004) Contribution of fine-scale vertical structure and swimming behaviour to formation of plankton layers on Georges Bank. *Mar Ecol Prog Ser* 267:27–43
- Garcés E, Masó M, Camp J (1999) A recurrent and localized dinoflagellate bloom in a Mediterranean beach. *J Plankton Res* 21:2373–2391
- Gentien P, Lunven M, Lehaître M, Duvent JL (1995) In-situ depth profiling of particle sizes. *Deep Sea Res I* 42:1297–1312
- Holligan PM (1979) Dinoflagellate blooms associated with tidal fronts around the British Isles. In: Taylor DL, Seliger HH (eds) Toxic dinoflagellate blooms. Elsevier, New York, pp 249–256
- Huisman J, Arrayás M, Ebert U, Sommeijer B (2002) How do sinking phytoplankton species manage to persist? *Am Nat* 159:245–254
- Jones KJ, Gowen RJ (1990) Influence of stratification and irradiance regime on summer phytoplankton composition in coastal and shelf seas of the British Isles. *Est Coast Shelf Sci* 30:557–567
- Juhl AR, Latz MI (2002) Mechanisms of fluid shear-induced inhibition of population growth in a red-tide dinoflagellate. *J Phycol* 38:683–694
- Kamykowski D (1981) The simulation of a California red tide using characteristics of a simultaneously measured internal wave field. *Ecol Model* 12:253–265
- Kamykowski D, Yamazaki H, Yamazaki AK, Kirkpatrick GJ (1998) A comparison of how different orientation behaviours influence dinoflagellate trajectories and photoreponses in turbulent water columns. In: Anderson DM, Cembella AD, Hallegraeff GM (eds) Physiological ecology of harmful algal blooms. NATO ASI Series 41. Springer, Berlin Heidelberg New York, pp 581–599
- Karp-Boss L, Boss E, Jumars PA (1996) Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. *Oceanogr Mar Biol Annu Rev* 34:71–109
- Karp-Boss L, Boss E, Jumars PA (2000) Motion of dinoflagellates in a simple shear flow. *Limnol Oceanogr* 45:1594–1602
- Kononen K, Huttunen M, Hällfors S, Gentien P, Lunven M, Huttula T, Laanemets J, Lilover M, Pavelson J, Stips A (2003) Development of a deep chlorophyll maximum of *Heterocapsa triquetra* Ehrenb. at the entrance of Gulf of Finland. *Limnol Oceanogr* 48:594–607
- Margalef R (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol Acta* 1:493–509
- Margalef R, Estrada M, Blasco D (1979) Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In: Taylor DL, Seliger HH (eds) Toxic dinoflagellate blooms. Elsevier, New York, pp 89–94
- Nielsen TG, Kiørboe T, Bjørnson PK (1990) Effects of a *Chrysochromulina polylepis* subsurface bloom on the planktonic community. *Mar Ecol Prog Ser* 62:21–35
- Pingree RD, Pugh PR, Holligan PM, Forster GR (1975) Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature* 258:672–677
- Pitcher GC, Boyd AJ (1996) Cross-shelf and along-shore dinoflagellate distributions and the mechanism of red tide formation within the southern Benguela upwelling system. In: Yasumoto T, Oshima Y, Fukuyo Y (eds) Harmful and toxic algal blooms. IOC -UNESCO, Paris, pp 243–246

- Pitcher GC, Weeks SJ (2006) The variability and potential for prediction of harmful algal blooms in the southern Benguela ecosystem. In: Shannon V et al (eds) *Benguela: predicting a large marine ecosystem*
- Pitcher GC, Boyd AJ, Horstman DA, Mitchell-Innes BA (1998) Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. *Mar Ecol Prog Ser* 172:253–264
- Raine R, McMahon T (1998) Physical dynamics on the continental shelf off southwestern Ireland and their influence on coastal phytoplankton blooms. *Cont Shelf Res* 18:883–914
- Rines JEB, Donaghay PL, Dekshenieks MM, Sullivan JM, Twardowski MS (2002) Thin layers and camouflage: hidden *Pseudo-nitzschia* spp. (Bacillariophyceae) populations in a fjord in the San Juan Islands, Washington, USA. *Mar Ecol Prog Ser* 225:123–137
- Seliger HH, Carpenter JH, Loftus M, McElroy WD (1970) Mechanisms for the accumulation of high concentration of dinoflagellates in a Bioluminescent Bay. *Limnol Oceanogr* 15:234–245
- Sellner KG (1997) Physiology, ecology, and toxic properties of marine cyanobacteria blooms. *Limnol Oceanogr* 42:1089–1104
- Smayda TJ, Reynolds CS (2001) Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *J Plankton Res* 23:447–461
- Sullivan JM, Swift E, Donaghay PL, Rines JEB (2003) Small-scale turbulence affects the division rate and morphology of two red-tide dinoflagellates. *Harmful Algae* 2:183–199
- Tester PA, Steidinger K (1997) *Gymnodinium breve* red tide blooms: initiation, transport, and consequences of surface circulation. *Limnol Oceanogr* 42:1039–1051
- Tilstone GH, Figueiras FG, Fraga F (1994) Upwelling-downwelling sequences in the generation of red tides in a coastal upwelling system. *Mar Ecol Prog Ser* 112:241–253
- Trainer VL, Hickey BM, Horner RA (2002) Biological and physical dynamics of domoic acid production off the Washington coast. *Limnol Oceanogr* 47:1438–1446
- Tyler MA, Seliger HH (1981) Selection for a red tide organism: physiological responses to the physical environment. *Limnol Oceanogr* 26:310–324
- Venrick EL (1999) Phytoplankton species structure in the central North Pacific 1973–1996: variability and persistence. *J Plankton Res* 21:1029–1042
- Vila M, Masó M (2005) Phytoplankton functional groups and harmful algal species in anthropogenically impacted waters of the NW Mediterranean Sea. *Scientia Marina* 69:31–45
- Yamazaki H, Mackas DL, Denman KL (2002) Coupling small-scale physical processes with biology: towards a Lagrangian approach. In: Robinson AR, McCarthy JJ, Rothschild BJ (eds) *The sea: biological-physical interactions in the sea*, vol 12. Wiley, New York, pp 51–112
- Zingone A, Wyatt T (2005) Harmful algal blooms: keys to the understanding of phytoplankton ecology. In: Robinson AR, Brink KH (eds) *The sea: ideas and observations on progress in the study of the seas*, vol 13. Harvard University Press, Harvard, pp 867–926
- Zirbel MJ, Veron F, Latz MI (2000) The reversible effect of flow on the morphology of *Ceratocorys horrida* (Peridinales, Dinophyta). *J Phycol* 36:46–58