

Pseudo-nitzschia blooms and physical oceanography off Washington State, USA

R. A. Horner , B. M. Hickey & J. R. Postel

To cite this article: R. A. Horner , B. M. Hickey & J. R. Postel (2000) *Pseudo-nitzschia* blooms and physical oceanography off Washington State, USA, South African Journal of Marine Science, 22:1, 299-308, DOI: [10.2989/025776100784125771](https://doi.org/10.2989/025776100784125771)

To link to this article: <https://doi.org/10.2989/025776100784125771>



Published online: 08 Apr 2010.



Submit your article to this journal [↗](#)



Article views: 330



View related articles [↗](#)



Citing articles: 1 View citing articles [↗](#)

PSEUDO-NITZSCHIA BLOOMS AND PHYSICAL OCEANOGRAPHY OFF WASHINGTON STATE, USA

R. A. HORNER*, B. M. HICKEY* and J. R. POSTEL*

Blooms of harmful algal species occur along the Washington coast, usually as a fraction of the total phytoplankton population. Although more than 20 potentially harmful species have been identified along that coast, the most deleterious effects on public health and the economy are from *Pseudo-nitzschia* spp. and *Alexandrium catenella*. During three surveys conducted in early summer 1996, 1997 and 1998, high concentrations of *Pseudo-nitzschia* spp. (values of up to 10^6 cells·L⁻¹, but generally $<10^5$ cells·L⁻¹) were present. *P. pungens* was dominant in 1996, whereas *P. pseudodelicatissima* was most abundant in 1997 and 1998. *A. catenella* was rare and in low concentrations (usually $<10^4$ cells·L⁻¹). Patterns of phytoplankton distributions during each survey appear to be closely related to upwelling and downwelling conditions prior to the survey.

The Pacific coastal waters off Washington are influenced by an eastern boundary current, the California Current. It is a broad, shallow, slow-moving current that flows southwards and brings cold, low-salinity, highly oxygenated, nutrient-rich subarctic water to the region. Prevailing winds and currents show marked seasonal variations. Currents flow generally northwards during autumn and winter, associated with on-shore flow near the surface and southwards during spring and summer, associated with offshore flow in the surface layers (Strub *et al.* 1987). However, within any season, wind and/or currents can reverse from the seasonal mean direction for periods of several days or more. Furthermore, the principal wind and current fluctuations are similar over distances of a few hundred kilometres along the coast, the currents being largely driven by wind (Hickey 1989, 1998).

There are marked seasonal variations in phytoplankton abundance over the narrow continental shelf off Washington. Highest cell concentrations are during spring and summer, typically inshore (Landry *et al.* 1989, Perry *et al.* 1989). A spring phytoplankton bloom occurs in March–April, initiated by increasing insolation and restratification of the upper layer, and summer phytoplankton blooms are driven by wind-induced, episodic upwelling of nutrient-rich water near the coast. Blooms that develop during intense upwelling, driven by north-westerly winds, may be advected rapidly towards the coast when winds relax and reverse their direction (Hermann *et al.* 1989). As a result, upwelling and downwelling play dominant roles in biological production.

Populations of toxic phytoplankton species along the Washington coast are contained within the seasonal variation in phytoplankton abundance. They are wide-

spread, occurring in coastal estuaries (Sayce and Horner 1996) as well as along open coastal beaches (present authors' unpublished data). However, toxic outbreaks along the west coast of the U.S. may be highly localized or extend over several hundred kilometres (Nishitani and Chew 1988, Price *et al.* 1991, Horner *et al.* 1997). Depending on the shellfish species affected, outbreaks may last for several months, even though the blooms that produce the toxins may be short-lived. For example, razor clams *Siliqua patula* may contain high levels of domoic acid for months (Drum *et al.* 1993, Horner *et al.* 1993, Wekell *et al.* 1998), whereas in laboratory studies blue mussels *Mytilus edulis* eliminate domoic acid within a few days (Novaczek *et al.* 1992). In field studies, however, depuration in blue mussels was slow, occurring over a period of about two months in late autumn when the water temperature fell rapidly and when numbers of *Pseudo-nitzschia* declined (Smith *et al.* 1990).

There are few long-term records of phytoplankton abundance for western Washington waters, and most of the current information on harmful algal blooms is gained from incidences of toxins in shellfish rather than from knowledge of toxic phytoplankton species. Dinoflagellates of the genus *Alexandrium* and diatoms of the genus *Pseudo-nitzschia* appear to pose the most pressing public health and economic problems in the region. Paralytic shellfish poisoning (PSP) has been found in all bivalve molluscs along the Washington coast beaches, at least since the 1940s when three people died after eating clams and mussels harvested in the area. PSP is usually highest in shellfish in July and August and most events occur between May and October. High levels of PSP, ranging from 286 to 341 µg toxin·100 g⁻¹ shellfish flesh (Washington

* School of Oceanography, Box 357940, University of Washington, Seattle, WA 98195-7940, USA. E-mail: rita@ocean.washington.edu

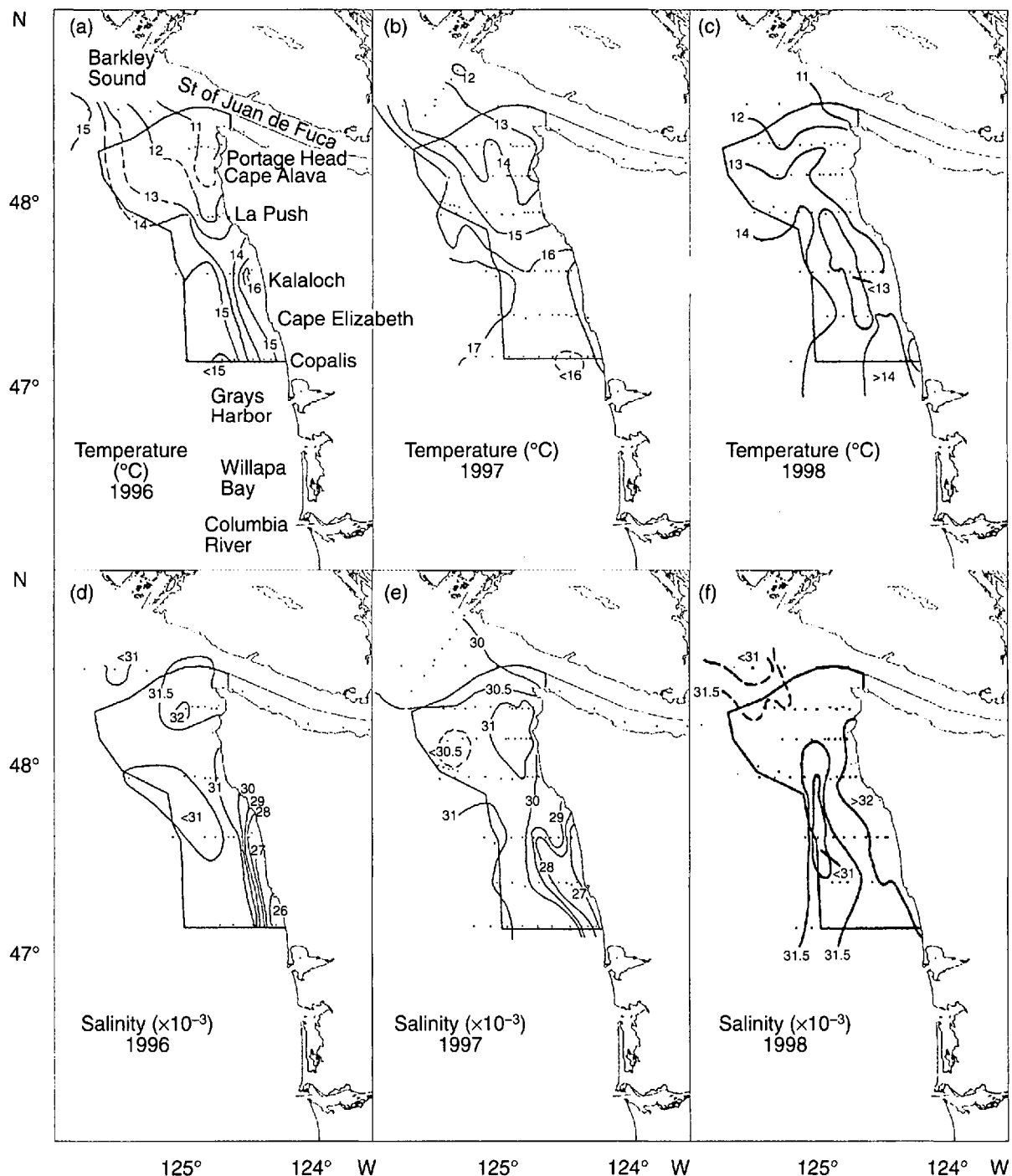


Fig. 1: Properties of the surface water during the surveys: temperature in (a) 1996, (b) 1997, (c) 1998, and salinity in (d) 1996, (e) 1997 and (f) 1998. Outlined area is the Olympic Coast National Marine Sanctuary

Department of Health, unpublished data), were found in commercially grown oysters in coastal estuaries in November and December 1997, yet razor clams on beaches surrounding the estuaries were not affected. Domoic acid poisoning (DAP), also called amnesic shellfish poisoning or ASP, was first recognized in the Pacific north-west in 1991 and has affected primarily recreationally harvested razor clams and commercially harvested Dungeness crabs *Cancer magister*. Although domoic acid is most common in razor clams in October and November, it has also been detected in the water column in association with *Pseudo-nitzschia* blooms off the northern Washington coast in July (Wekell et al. 1998). In October 1998, domoic acid levels in razor clams on open beaches were the highest ever detected there (up to $287 \mu\text{g}\cdot\text{g}^{-1}$ of shellfish flesh – Washington Department of Health, unpublished data) and resulted in the cancellation of the recreational harvest of razor clams. Traces of domoic acid (approx. $1\text{--}2 \mu\text{g}\cdot\text{g}^{-1}$) were also found in commercially grown oysters in the coastal estuaries. Therefore, toxin outbreaks cause substantial economic losses to the coastal communities, as well as being a serious public health risk. In order to protect the public, blanket closures of the Washington coast are in effect from spring to autumn each year for PSP and sometimes seasonally (spring and/or autumn) for DAP. Such closures are necessary because there is little understanding of the environmental conditions and other factors that lead to the presence of toxin-producing algal species.

To address these issues, data were collected on three surveys in the Olympic Coast National Marine Sanctuary off the northern Washington coast (Fig. 1). In addition, samples were collected at five beaches, three within the Sanctuary, approximately twice monthly for four years. This paper reports primarily on the offshore distribution and abundance of phytoplankton species that are known toxin producers (e.g. species of *Pseudo-nitzschia* and *Alexandrium*), and on the total diatom population during the surveys.

MATERIAL AND METHODS

Samples were taken during three cruises: 27 June–9 July 1996, 7–20 July 1997 and 25 June–3 July 1998. Cross-shelf transects were occupied from south to north on the first two cruises, and from north to south during the third cruise. Data were usually collected at night, with each transect taking about 8–10 h to complete. Temperature and salinity data were collected at each station by means of a CTD cast to within 5–10 m of the bottom. Phytoplankton, nutrient and salinity samples

were collected at 4–6 depths in the upper 50 m of the water using Niskin bottles attached to the CTD rosette. Phytoplankton samples were preserved with buffered formalin (c. 1% final concentration) and analysed for species presence and abundance by the Utermöhl inverted microscope method (Hasle 1978). Identifications of *Pseudo-nitzschia* spp. were confirmed for two cruises using scanning electron microscopy (SEM) on selected samples collected by vertical net tows (20- μm mesh, 25-cm mouth diameter) in the upper 10 m. Nutrient samples were frozen and later analysed using standard autoanalyser methods (Whitledge et al. 1981). To verify the calibration of the CTD conductivity sensor, the salinity of selected bottle samples was determined in the laboratory using a Guildline Autosol 8400B salinometer. Representative wind data for the region were obtained from the U.S. National Data Buoy Centre.

Additional information on species presence was obtained from shore sampling at five beaches on the central Washington coast. Samples were collected from the surf using a bucket, and the contents were concentrated with a 20- μm mesh net. In 1997, such collections were made at the nearshore end of the transects, within one day of being sampled during the cruise. Samples were examined using phase-contrast light microscopy within a day of collection, while the cells were still alive. Species were identified and their relative abundances determined. Some samples were acid-cleaned and examined by means of scanning electron microscopy (SEM) to positively identify *Pseudo-nitzschia* spp.

RESULTS

Data presented here are limited to near-surface measurements. In 1996 and 1997, colder, more saline water occurred to the north and warmer, less saline water to the south in the survey area. In 1998, however, the water was generally cooler and more saline close to shore over most of the study area (Fig. 1). Temperatures at all stations in 1997 exceeded those in 1996 and 1998, reflecting the *El Niño* conditions that existed in the Pacific north-west during 1997 (Huyer et al. 1998). In that year, warmer water was present in the southwestern corner of the Sanctuary.

Along the Washington coast, southerly winds are associated with onshore and northward surface flow over the shelf (generally downwelling conditions), and northerly winds are associated with offshore and southward surface flow (generally upwelling conditions – Hickey 1989). Time-series of wind vectors (Fig. 2) show that wind changed speed and direction over short time periods during each cruise. In 1996 and

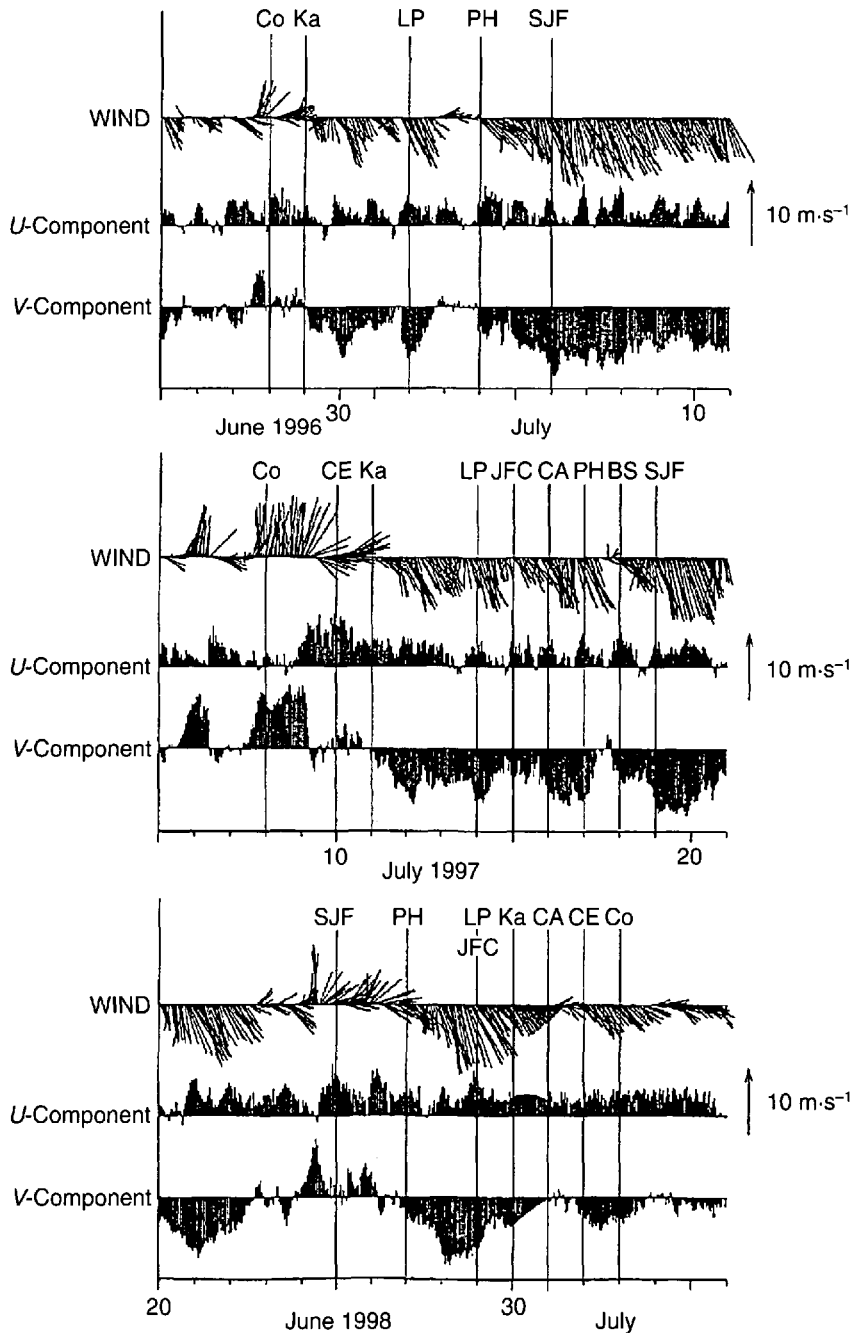


Fig. 2: Time-series showing representative regional winds off the Washington coast for each survey. Wind vectors point in the direction to which the wind blows. Onshore-offshore (U) and north-south (V) components are positive onshore and northward respectively. Dates on which particular transects were sampled are indicated on the time axis of each plot. Location abbreviations: Co = Copalis Beach, CE = Cape Elizabeth, Ka = Kalaloch, LP = La Push, JFC = Juan de Fuca Canyon, CA = Cape Alava, PH = Portage Head, BS = Barkley Sound, SJF = Strait of Juan de Fuca

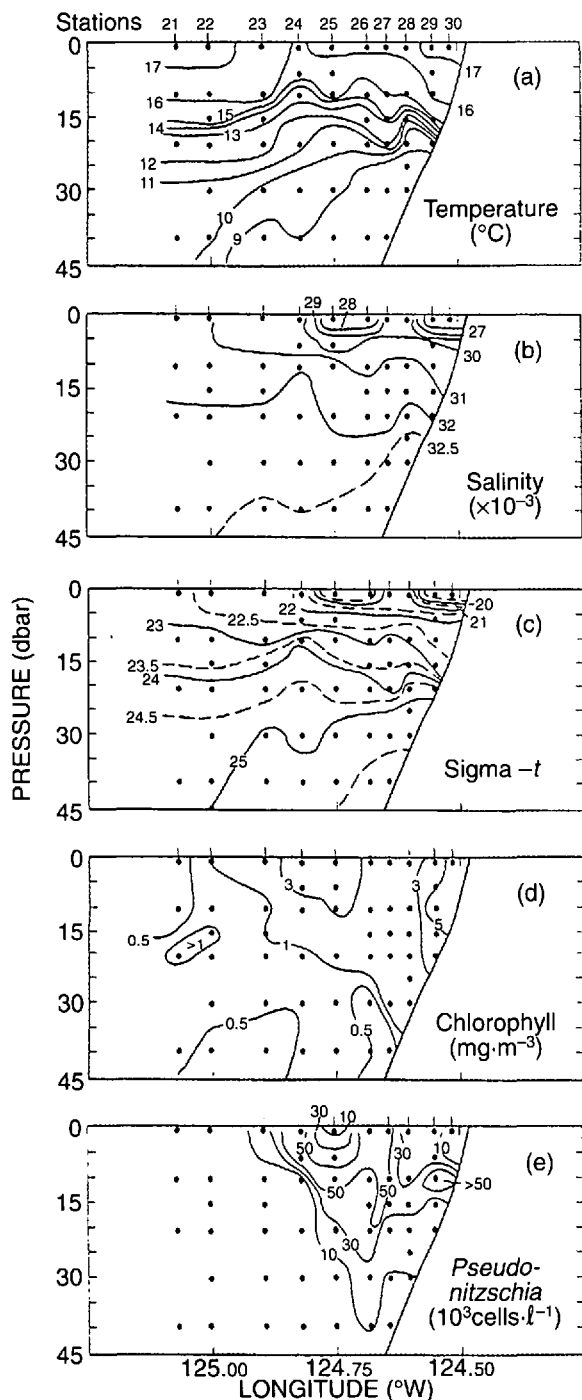


Fig. 3: Cross-shelf water properties off Kalaloch on 11 July 1997, following downwelling conditions: (a) temperature, (b) salinity, (c) sigma-t, (d) chlorophyll and (e) *Pseudo-nitzschia* spp. concentration

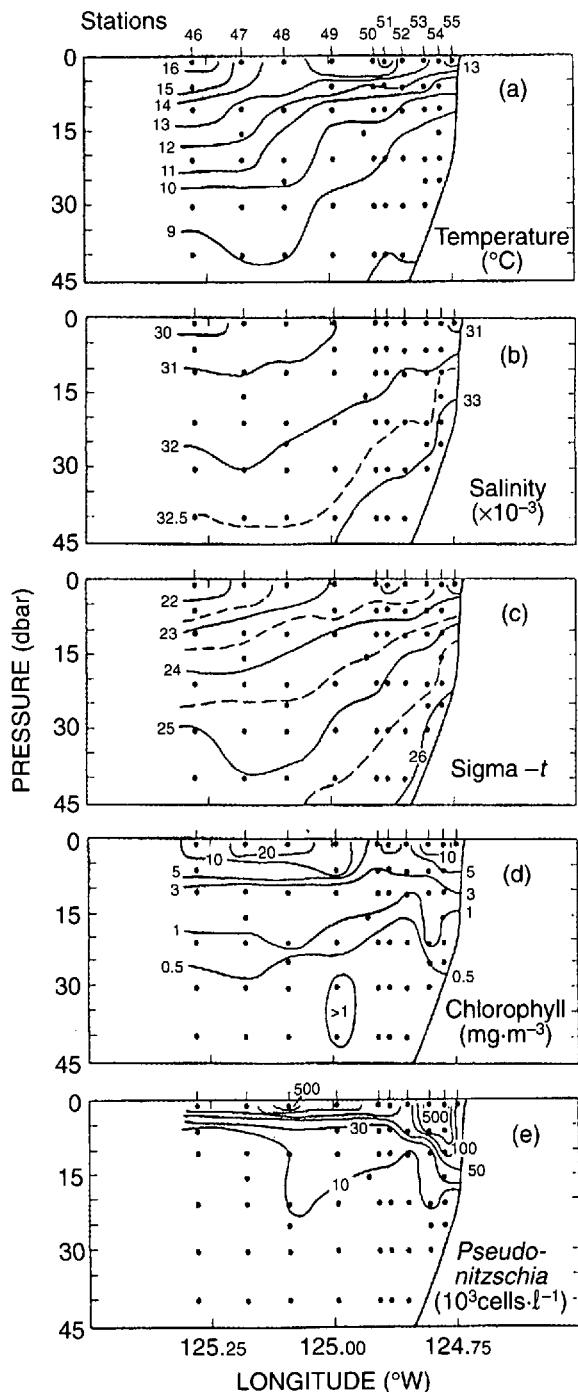


Fig. 4: Cross-shelf water properties off Cape Alava on 16 July 1997, following upwelling conditions: (a) temperature, (b) salinity, (c) sigma-t, (d) chlorophyll and (e) *Pseudo-nitzschia* spp. concentration

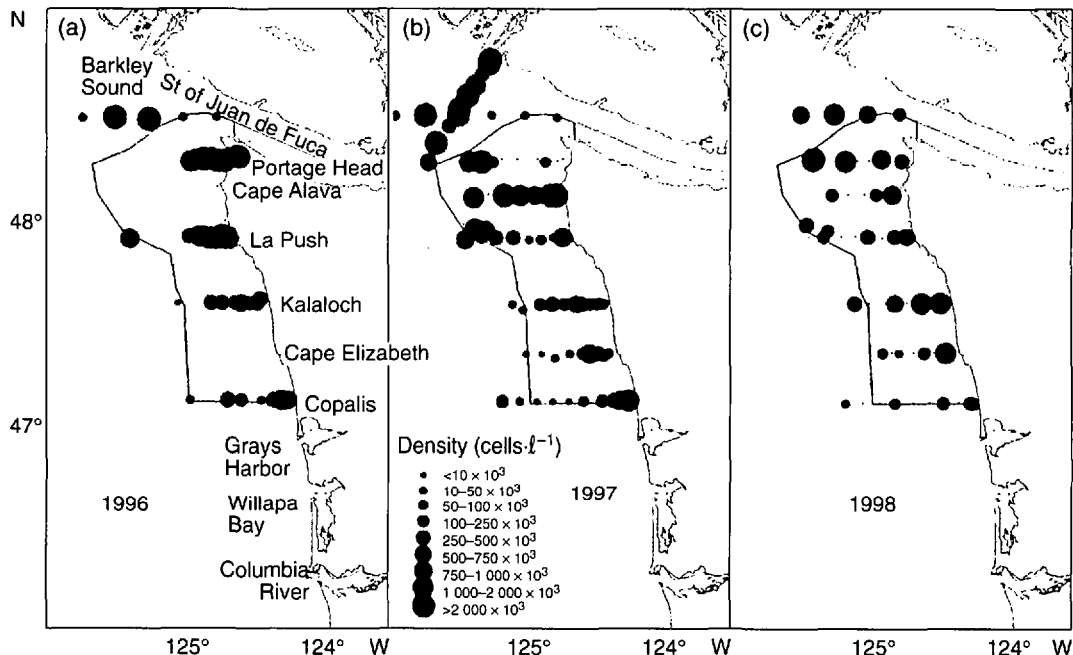


Fig. 5: Total diatom distributions and abundances at the surface for surveys in (a) 1996, (b) 1997 and (c) 1998. Small dots indicate station locations for samples not analysed

1997, the southern transects were sampled during periods of modest (1996) or strong (1997) southerly winds. The northern transects were occupied during a period of northerly winds, interrupted on several occasions by wind relaxation (zero to near zero winds) or by modest southerly winds. In 1998, the northernmost transect (Strait of Juan de Fuca) was sampled during a period of modest southerly winds, whereas most of the other transects were sampled during periods of relatively strong northerly winds (Fig. 2). Therefore, the warmer, fresher water at the southern stations in 1996 and 1997 was likely a result of northward and onshore movement of water from the coastal estuaries south of the Sanctuary (Fig. 1). The colder, more saline water nearshore and north of La Push in 1996 and 1997 was likely a result of the prevalence of upwelling. Nutrient concentrations also were consistent with upwelling conditions in the northern region. Near-surface concentrations were lower in the south than in the north. From south to north, phosphate values ranged from <0.1 to $2 \mu\text{mol}\cdot\text{L}^{-1}$, silicate from <1 to $45 \mu\text{mol}\cdot\text{L}^{-1}$, nitrate from 0 to $14 \mu\text{mol}\cdot\text{L}^{-1}$, and ammonium was generally $<1 \mu\text{mol}\cdot\text{L}^{-1}$. In 1998, coastal water properties were consistent with weak downwelling at the northern end of the survey, whereas there was relatively strong upwelling from La Push southwards (Fig. 1).

The structure of the water column along two cross-shelf sections (one during downwelling and the other during upwelling) occupied on 11 and 16 July 1997 is shown in Figures 3 and 4 respectively. The winds on 11 July off Kalaloch, and for the previous several days, were primarily southerly, which led to warmer, less saline waters near the coast, as well as depressed isotherms, isohalines and isopycnals. Higher chlorophyll concentrations appeared to be associated with two pockets of low salinity, near-surface water, one near-shore and the other midshelf, with a nearshore subsurface maximum ($5 \text{ mg}\cdot\text{m}^{-3}$). However, *Pseudo-nitzschia* spp. had a different spatial structure, with a band of high cell concentrations beneath less saline water and lower cell concentrations in two pockets of freshwater near the surface. This difference in structure may be attributable to the fact that total chlorophyll would include phytoplankton indigenous to (or previously entrained by) the estuarine plume water.

In contrast, during upwelling conditions on 16 July off Cape Alava, after several days of northerly winds (Fig. 4), the nearshore, near-surface water was $3\text{--}4^\circ\text{C}$ cooler and the salinity was $2\text{--}3 \times 10^{-3}$ higher than found off Kalaloch five days earlier. The chlorophyll distribution off Cape Alava had both higher surface concentrations ($10\text{--}20 \text{ mg}\cdot\text{m}^{-3}$) and steeper vertical gra-

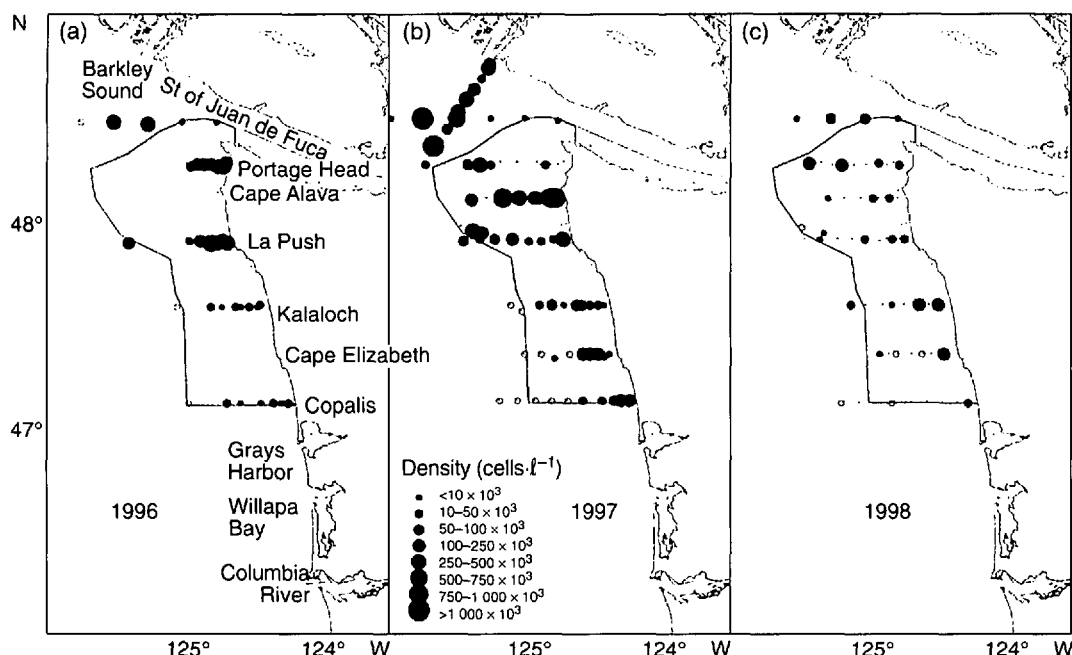


Fig. 6: Distribution and abundance of *Pseudo-nitzschia* spp. at the surface for surveys in (a) 1996, (b) 1997 and (c) 1998. Open circles represent samples in which *Pseudo-nitzschia* spp. cells were not present. Small dots indicate station locations for samples not analysed

dients than off Kalaloch. Also, concentrations of *Pseudo-nitzschia* spp. were 50 times higher at the surface (often $>3 \times 10^5$ cells·l⁻¹), but numbers dropped off sharply below 10 m at most stations. The nearshore maximum may be a result of new growth (five days of upwelling preceded sampling), whereas the maximum farther offshore may be a residual from a previous upwelling cycle.

Total diatom abundance was similar in all three years (Fig. 5), despite the fact that sampling in 1997 was conducted during a major *El Niño* event. *Pseudo-nitzschia* spp., however, appeared to be more abundant during the 1997 survey (Fig. 6).

Highest cell concentrations were generally in the upper 10–20 m of the water column, declining markedly below 30 m (Figs. 3, 4). *Pseudo-nitzschia* spp. were found in $>85\%$ of the samples, but they generally constituted $<10\%$ of the phytoplankton population. *P. pungens* was most abundant in 1996 and *P. pseudodelicatissima* was the dominant species in 1997 and 1998, when few *P. pungens* cells were present. However, during the autumn 1998 DAP outbreak, three species of *Pseudo-nitzschia* (*P. pseudodelicatissima*, *P. pungens* and *P. fraudulenta*) were identified in the beach samples and in additional samples collected just offshore

from Grays Harbor. All species are reported to produce domoic acid (Martin et al. 1990, 1993, Rhodes et al. 1998, Trainer et al. 1998, Bates et al. 1998), although cellular levels of DA may be low.

Alexandrium catenella was never abundant during the surveys, being present in only 11% of the samples, and usually at concentrations of about 10^4 cells·l⁻¹ (Fig. 7). The species was distributed over the whole area in 1996 and 1997, but was confined mostly to the central and southern part of the survey area in 1998. *A. catenella* was also more abundant in 1997. The patch of warmer water in the south-western corner of the Sanctuary in 1997 contained no *Pseudo-nitzschia* spp. or *A. catenella* cells. This patch of anomalously warm water was likely associated with *El Niño* conditions and was probably advected northwards and onshore by the strong downwelling event during 8 and 9 July 1997 (Fig. 2).

DISCUSSION

Off southern California, *Pseudo-nitzschia* spp., especially *P. australis*, have been a regular and abun-

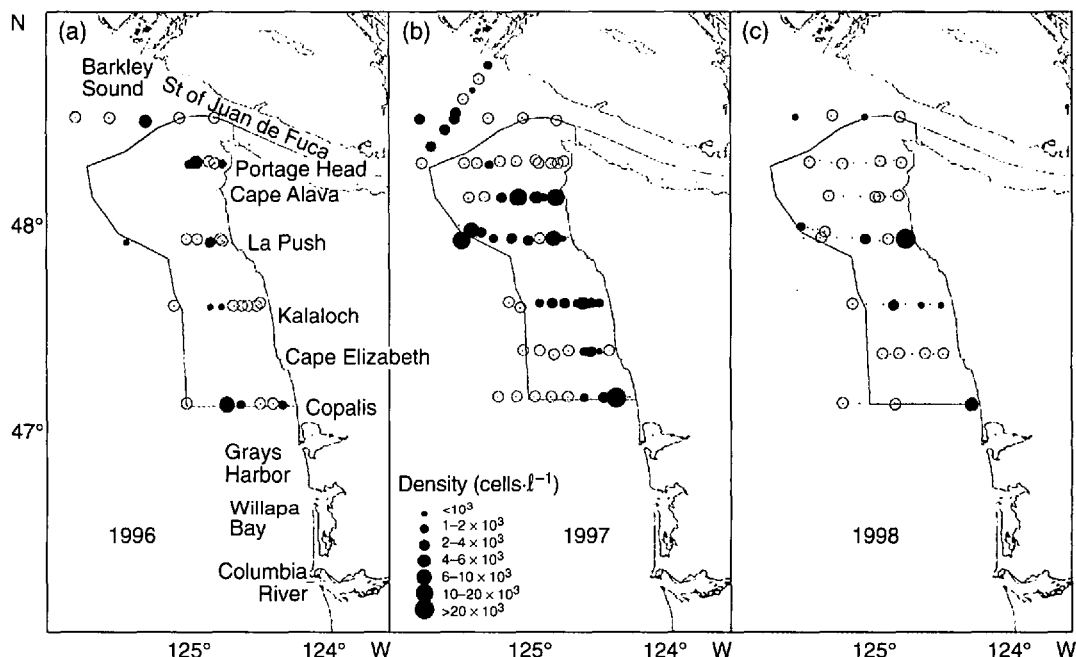


Fig. 7: Distribution and abundance of *A. catenella* (all cells counted regardless of depth are plotted) for surveys in (a) 1996, (b) 1997 and (c) 1998. Large dot nearshore at La Push (1998) was one 15-celled chain seen at 30 m. Open circles represent samples in which no *A. catenella* cells were seen; small dots indicate station locations for samples not analysed

dant component of the phytoplankton in spring and early summer since the 1930s (Lange *et al.* 1994). Periods of high abundance were associated with the intrusion of cool, high-nutrient water, possibly associated with upwelling. Farther north, in Monterey Bay, Buck *et al.* (1992) found *P. australis* to be positively correlated with warmer water, but also with weak upwelling events. Historical data for Monterey Bay (e.g. Bolin and Abbott 1963, Garrison 1979, Schrader 1981, Smith 1991) suggest that *Pseudo-nitzschia* spp. may bloom throughout the year. However, Walz *et al.* (1994) found blooms only in late summer and autumn, when seasonal, coastal upwelling is sporadic and hydrographic conditions are characterized by warm water and low nutrients.

It appears that populations of *Pseudo-nitzschia* spp. and *Alexandrium catenella* are frequently present off the Washington coast, but not always in high concentrations. Higher cell densities of these species in 1997 may be attributable to the warmer water or increased stratification associated with *El Niño* conditions. The lower cell densities in 1998 may be a reflection of the short duration of upwelling during the survey. It was therefore uncertain if cell densities were specifically related to *El Niño* conditions.

The spatial distributions of total diatoms, as well as of *Pseudo-nitzschia* spp., seem to be strongly related to the direction of coastal cross-shelf currents and to the upwelling of nutrients. During periods of persistent upwelling and offshore flow, high cell densities were generally found far offshore. Onshore advection during downwelling resulted in lower densities (both total diatoms and *Pseudo-nitzschia* spp.) offshore during the 1996 and 1997 surveys from Copalis to Kalaloch (see Kalaloch transect, 1997 – Figs 3, 5, 6, and the Cape Elizabeth transect during a relaxation event in 1998 – Figs 2, 5, 6). Recent upwelling was consistent with increased cell densities nearshore (La Push and Cape Alava transects, 1997 – Figs 4, 5, 6) and possibly new cell growth (density 500×10^3 cells·l⁻¹ at Cape Alava) in response to increased nutrient concentrations.

In 1997, there was a bloom of *P. pungens* at a site just south of Grays Harbor (outside the Sanctuary). This was ascertained from beach collections taken when the southern transects were sampled (i.e. 8 and 10 July), and when cell density was high. This suggests that the cells that grew over the adjacent continental shelf were advected toward the coast, most likely as a result of downwelling. This documents the first example

in which an offshore bloom has been related to a bloom so close to shore. The nearshore bloom was short-lived, lasting only a few days, and reflects the dynamic ocean circulation (in particular, episodic upwelling and downwelling over the adjacent shelf) of the area. An oomycete fungus present in some cells on 10 July may have contributed to the decline of this bloom (see also Pauley *et al.* 1994, Elbrächter and Schnepf 1998). Despite the appearance of the bloom in the surf zone, no domoic acid was found in razor clams harvested from the same beach on 8 July, one day after the start of the downwelling event.

The distribution of *A. catenella* in this study area remains puzzling. Few cells were observed in the samples; the high concentration at La Push in 1998 (Fig. 7) was the result of one 15-celled chain from 30 m deep. Usually only one or two cells were present and chains were rare. More cells were observed in 1997, during the *El Niño* event. *A. catenella* were observed in all three years of study, generally in the upwelling season. PSP outbreaks in northern California occur primarily in autumn, following relaxation of upwelling (Horner *et al.* 1997, D. M. Anderson, Woods Hole Oceanography Institution, unpublished data). Similar observations have been made in the rias of north-western Spain (Fraga *et al.* 1988) and the Benguela upwelling region (Pitcher and Boyd 1996, Pitcher *et al.* 1998, Probyn *et al.* 2000). Perhaps the same situation occurred in November–December of 1997, which led to the extensive PSP outbreak in Washington's coastal estuaries. If so, then the relatively small *A. catenella* population observed offshore in July 1997 probably was maintained until late autumn, when changes in hydrographic conditions favoured increased growth and transport to the estuaries.

Although diatoms producing domoic acid appear regularly off the Pacific north-west coast, the link between their presence offshore and the incidence of domoic acid in razor clams has not been demonstrated. It is shown here that *A. catenella* is frequently present off the Washington coast, albeit in relatively small numbers, but the mechanisms that maintain and transport cells to the coastal estuaries are unknown. The following important questions need to be addressed:

- (i) Are blooms of toxin-producing algae initiated offshore, and if so, how?
- (ii) What is the mechanism and frequency of transport to coastal beaches and estuaries?
- (iii) What is the relationship between toxic blooms and toxin accumulation in coastal shellfish?

Appropriate research is being implemented, using ships of opportunity (e.g. the Sanctuary-sponsored surveys), to gain relevant information towards addressing these important questions.

ACKNOWLEDGEMENTS

This work was funded in part by grants NA66FD0113, NA86FD0393 and 40ABNC801574 from the National Oceanic and Atmospheric Administration (NOAA) to the University of Washington. We thank Messrs E. Bowlby and G. Galassos of the Olympic Coast National Marine Sanctuary, the captain and crew of the NOAA research vessel *McArthur*, and Ms S. Geier, Dr N. Kachel and Mr P. Rudell of the School of Oceanography for their help with sampling and data processing. The views expressed here are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

LITERATURE CITED

- BATES, S. S., GARRISON, D. L. and R. A. HORNER 1998 — Bloom dynamics and physiology of domoic-acid-producing *Pseudo-nitzschia* species. In *Physiological Ecology of Harmful Algal Blooms*. Anderson, D. M., Cembella, A. D. and G. M. Hallegraeff (Eds). Heidelberg; Springer: 267–292.
- BOLIN, R. L. and D. P. ABBOTT 1963 — Studies on the marine climate and phytoplankton of the central coast area of California, 1954–1960. *Rep. Calif. coop. ocean. Fish. Invest.* 9: 23–45.
- BUCK, K. R., UTTAL-COOKE, L., PILSKALN, C. H., ROELKE, D. L., VILLAC, M. C., FRYXELL, G. A., CIFUENTES, L. and F. P. CHAVEZ 1992 — Autecology of the diatom *Pseudonitzschia australis*, a domoic acid producer, from Monterey Bay, California. *Mar. Ecol. Prog. Ser.* 84: 293–302.
- DRUM, A. S., SIEBENS, T. L., CRECELIUS, E. A. and R. A. ELSTON 1993 — Domoic acid in the Pacific razor clam *Siliqua patula* (Dixon, 1789). *J. Shellfish Res.* 12: 443–450.
- ELBRÄCHTER, M. and E. SCHNEPF 1998 — Parasites of harmful algae. In *Physiological Ecology of Harmful Algal Blooms*. Anderson, D. M., Cembella, A. D. and G. M. Hallegraeff (Eds). Heidelberg; Springer: 351–363.
- FRAGA, S., ANDERSON, D. M., BRAVO, I., REGUERA, B., STEIDINGER, K. A. and C. M. YENTSCH 1988 — Influence of upwelling relaxation on dinoflagellates and shellfish toxicity in Ria de Vigo, Spain. *Estuar. coast. Shelf Sci.* 27: 349–361.
- GARRISON, D. L. 1979 — Monterey Bay phytoplankton. 1. Seasonal cycles of phytoplankton assemblages. *J. Plank. Res.* 3: 241–256.
- HASLE, G. R. 1978 — The inverted-microscope method. In *Phytoplankton Manual*. Sournia, A. (Ed.). Unesco Monographs on Oceanographic Methodology 6: 88–96.
- HERMANN, A., HICKEY, B. M., LANDRY, M. R. and D. WINTER 1989 — Coastal upwelling dynamics. In *Coastal Oceanography of Washington and Oregon*. Landry, M. R. and B. M. Hickey (Eds). Amsterdam; Elsevier: 211–253.
- HICKEY, B. M. 1989 — Patterns and processes of circulation over the Washington continental shelf and slope. In *Coastal Oceanography of Washington and Oregon*. Landry, M. R. and B. M. Hickey (Eds). Amsterdam; Elsevier: 41–115.
- HICKEY, B. M. 1998 — Coastal oceanography of western North America from the tip of Baja California to Vancouver Island. Coastal segment (8, E). In *The Sea* 11. Robinson, A. R. and K. H. Brink (Eds). New York; Wiley: 345–393.

- HORNER, R. A., GARRISON, D. L. and F. G. PLUMLEY 1997 — Harmful algal blooms and red tide problems on the U.S. west coast. *Limnol. Oceanogr.* **42**: 1076–1088.
- HORNER, R. A., KUSSKE, M. B., MOYNIHAN, B. P., SKINNER, R. N. and J. C. WEKELL 1993 — Retention of domoic acid by Pacific razor clams, *Siliqua patula* (Dixon, 1789): preliminary study. *J. Shellfish Res.* **12**: 451–456.
- HUYER, A., BARTH, J. A., FLEISCHBEIN, J., KOSRO, P. M. and R. L. SMITH 1998 — The coastal ocean off Oregon and northern California during the 1997–8 *El Niño*. I. Temperature, salinity, and geostrophic velocity fields. *Eos* **79**(45): p. F485.
- LANDRY, M. R., POSTEL, J. R., PETERSON, W. K. and J. NEWMAN 1989 — Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon shelf. In *Coastal Oceanography of Washington and Oregon*. Landry, M. R. and B. M. Hickey (Eds). Amsterdam; Elsevier: 1–40.
- LANGE, C. B., REID, F. M. H. and M. VERNET 1994 — Temporal distribution of the potentially toxic diatom *Pseudonitzschia australis* at a coastal site in southern California. *Mar. Ecol. Prog. Ser.* **104**: 309–312.
- MARTIN, J. L., HAYA, K., BURRIDGE, L. E. and D. J. WILDISH 1990 — *Nitzschia pseudodelicatissima* – a source of domoic acid in the Bay of Fundy, eastern Canada. *Mar. Ecol. Prog. Ser.* **67**: 177–182.
- MARTIN, J. L., HAYA, K. and D. J. WILDISH 1993 — Distribution and domoic acid content of *Nitzschia pseudodelicatissima* in the Bay of Fundy. In *Toxic Phytoplankton Blooms in the Sea*. Smayda, T. J. and Y. Shimizu (Eds). Amsterdam; Elsevier: 613–618.
- NISHITANI, L. and K. K. CHEW 1988 — PSP toxins in the Pacific coast states: monitoring programs and effects on bivalve industries. *J. Shellfish Res.* **7**: 653–669.
- NOVACEK, I., MADHYASTHA, M. S., ABLETT, R. F., DONALD, A., JOHNSON, G., NIJJAR, M. S. and D. E. SIMS 1992 — Depuration of domoic acid from live blue mussels (*Mytilus edulis*). *Can. J. Fish. Aquat. Sci.* **49**: 312–318.
- PAULEY, K. E., FRITZ, L., STRONGMAN, D., O'NEIL, D. and J. C. SMITH 1994 — Parasitism of *Pseudonitzschia pungens* by a marine fungus. In *Proceedings of the Fourth Canadian Workshop on Harmful Marine Algae*. Forbes, J. R. (Ed.). *Can. tech. Rep. Fish. Aquat. Sci.* **2016**: p. 28.
- PERRY, M. J., BOLGER, J. P. and D. C. ENGLISH 1989 — Primary production in Washington coastal waters. In *Coastal Oceanography of Washington and Oregon*. Landry, M. R. and B. M. Hickey (Eds). Amsterdam; Elsevier: 117–138.
- PITCHER, G. C. and A. J. BOYD 1996 — Across-shelf and along-shore dinoflagellate distributions and the mechanisms of red tide formation within the southern Benguela upwelling system. In *Harmful and Toxic Algal Blooms*. Yasumoto, T., Oshima, Y. and Y. Fukuyo (Eds). Paris; Intergovernmental Oceanographic Commission of UNESCO: 243–246.
- PITCHER, G. C., BOYD, A. J., HORSTMAN, D. A. and B. A. MITCHELL-INNES 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.
- PRICE, D. W., KIZER, K. W. and K. H. HANSGEN 1991 — California's paralytic shellfish poisoning prevention program, 1927–89. *J. Shellfish Res.* **10**: 119–145.
- PROBYN, T. A., PITCHER, G. C., MONTEIRO, P. M. S., BOYD, A. J. and G. NELSON 2000 — Physical processes contributing to harmful algal blooms in Saldanha Bay, South Africa. *S. Afr. J. mar. Sci.* **22**: 285–297.
- RHODES, L., SCHOLIN, C., GARTHWAITE, I., HAYWOOD, A. and A. THOMAS 1998 — Domoic acid producing *Pseudo-nitzschia* species educed by whole cell DNA probe-based and immunochemical assays. In *Harmful Algae*. Reguera, B., Blanco, J., Fernández, M. L. and T. Wyatt (Eds). Paris; Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO: 274–277.
- SAYCE, K. and R. A. HORNER 1996 — *Pseudo-nitzschia* spp. in Willapa Bay, Washington, 1992 and 1993. In *Harmful and Toxic Algal Blooms*. Yasumoto, T., Oshima, Y. and Y. Fukuyo (Eds). Paris; Intergovernmental Oceanographic Commission of UNESCO: 131–134.
- SCHRADER, G. C. 1981 — Seasonal cycles of phytoplankton in relation to the hydrography of Monterey Bay. *Tech. Rep. Moss Landing Mar. Lab.* **81-2**: 1–92.
- SMITH, P. L. 1991 — Effects of the 1982–1983 *El Niño* on phytoplankton populations in Monterey Bay, California. M.Sc. thesis, University of California, Santa Cruz: 149 pp.
- SMITH, J. C., CORMIER, R., WORMS, J., BIRD, C. J., QUILLIAM, M. A., POCKLINGTON, R., ANGUS, R. and L. HANIC 1990 — Toxic blooms of the domoic acid containing diatom *Nitzschia pungens* in the Cardigan River, Prince Edward Island, in 1988. In *Toxic Marine Phytoplankton*. Granéli, E., Sundström, B., Edler, L. and D. M. Anderson (Eds). New York; Elsevier: 227–232.
- STRUB, P. T., ALLEN, J. S., HUYER, A., SMITH, R. L. and R. C. BEARDSLEY 1987 — Seasonal cycles of currents, temperatures, winds and sea level over the northeast Pacific continental shelf: 35°N–48°N. *J. geophys. Res.* **92**: 1507–1526.
- TRAINER, V. L., WEKELL, J. C., HORNER, R. A., HATFIELD, C. L. and J. E. STEIN 1998 — Domoic acid production by *Pseudo-nitzschia pungens*. In *Harmful Algae*. Reguera, B., Blanco, J., Fernández, M. L. and T. Wyatt (Eds). Paris; Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO: 337–340.
- WALZ, P. M., GARRISON, D. L., GRAHAM, W. M., CATTEY, M. A., TJEERDEMA, R. S. and M. W. SILVER 1994 — Domoic acid-producing diatom blooms in Monterey Bay, California: 1991–1993. *Natural Toxins* **2**: 271–279.
- WEKELL, J. C., HORNER, R. A., POSTEL, J. R., HATFIELD, C. L., ROSS, A. M. and V. L. TRAINER 1998 — *In situ* domoic acid levels in *Pseudo-nitzschia* cells off the Washington state coast in July 1996. In *Harmful Algae*. Reguera, B., Blanco, J., Fernández, M. L. and T. Wyatt (Eds). Paris; Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO: 235–236.
- WHITLEDGE, T. E., MALLOY, S. C., PATTON, C. J. and C. D. WIRICK 1981 — Automated nutrient analysis in seawater. *Rep. Brookhaven nat. Lab.* **51398**: 216 pp.