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Biodiversity, biogeography and potential trophic impact of *Protoperidinium* spp. (Dinophyceae) off the southwestern coast of Ireland

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This study is the first detailed investigation of the diversity, distribution and potential grazing impacts of Protoperidinium spp. in relation to the hydrography and phytoplankton distributions off the southwestern coast of Ireland. In late July 2003, the area was well stratified, and the Irish Shelf Front was apparent as a strong salinity front offshore. Thirty-two species of Protoperidinium were identified and classified as nearshore, offshore and widespread, based on distribution. In the Celtic Sea, phototrophic dinoflagellates dominated the plankton community nearshore, whereas diatoms dominated offshore of the Irish Shelf Front. Protoperidinium species, including P. steinii, P. depressum and the putative azaspiracid-toxin producer, P. crassipes, were most abundant nearshore in the Celtic Sea. The Bantry Bay section had the highest concentration and diversity of plankton in the study area. Most Protoperidinium species had the highest abundance nearshore along the Bantry Bay section, but the highest concentration of P. crassipes was offshore. Given the plankton concentrations and estimated grazing rates of Protoperidinium species, Protoperidinium had the potential to consume 30–80% of the dinoflagellate or diatom standing stock at the time of the study.

INTRODUCTION

The designation of *Protoperidinium crassipes* as the putative source of azaspiracid (AZA) shellfish toxin off the coast of Ireland (James *et al.*, 2003) renewed research interest in the dinoflagellate genus *Protoperidinium*. Although more than 200 *Protoperidinium* species (Balech, 1974) have been identified from waters around the world, little is known about the ecologies of species in this genus of marine, thecate, heterotrophic dinoflagellates.

Laboratory studies and observations of live field samples have shown that *Protoperidinium* consume their prey through a unique mechanism wherein the dinoflagellate envelops its prey in a pseudopod, called the pallium, in which digestion occurs external to the *Protoperidinium* cell (Gaines and Taylor, 1984; Jacobson and Anderson, 1986). This technique allows *Protoperidinium* to consume prey items as large or larger than themselves, with the size ratio of *Protoperidinium* to their prey tending toward 1:1 or greater, depending upon the species (Naustvoll, 2000). *Protoperidinium* spp. feed primarily on medium to large diatoms and dinoflagellates, and thus compete with mesozooplankton for food resources. Small plankton, like flagellates and bacteria, are not consumed. Most *Protoperidinium* spp. studied to date have been shown in the laboratory to be species-specific selective feeders, whereas other *Protoperidinium* spp. feed and exhibit positive growth rates on a diversity of diatom and dinoflagellate species (Jacobson and Anderson, 1986; Jeong and Latz, 1994; Buskey, 1997; Naustvoll, 2000; Menden-Deuer *et al.*,

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2005). Some species will even feed on copepod eggs and nauplii or detritus, or resort to cannibalism, at least in culture, if other food resources are limited (Jeong and Latz, 1994; Jeong, 1996; Naustvoll, 2000).

The link between *P. crassipes* and AZA toxicity now appears tenuous, as production of AZA by this species has not been verified since the initial observation, and recent occurrences of azaspiracid shellfish poisoning (AZP) off the coast of Ireland have not been well correlated with the presence of the species (Moran *et al.*, 2005). The previous detection of AZA in *P. crassipes* cells but not in other dinoflagellate species (James *et al.*, 2003) suggests that if *P. crassipes* does not produce AZA endogenously, it may accumulate the toxin from selectively consumed phytoplankton prey. Either way, understanding the ecology and trophic role of *Protoperidinium* spp. may be important to comprehending the dynamics of toxic phytoplankton blooms and shellfish toxicity.

The bays along the southwestern coast of Ireland are important sites of shellfish and finfish aquaculture. Harmful algal blooms (HABs) causing shellfish toxicity heavily impact the region, however, leading to harvesting closures, large economic losses and threats to public health. The biology and hydrodynamics of some of these HABs (e.g. *Gymnodinium mikimotoi*, *Alexandrium* spp.) are now fairly well understood (Raine *et al.*, 1990, 1993; McMahon *et al.*, 1998; Raine *et al.*, 2001). In this area, the 200 m isobath lies ~55 km from the coast. The bathymetry leads to a salinity and temperature front, called the Irish Shelf Front, ~35 km offshore, which strongly influences plankton community structure and dynamics (Raine and McMahon, 1998). Little is known about the specific factors controlling the ecology of *Protoperidinium* in the region.

The ecologies of different *Protoperidinium* spp. are likely to be diverse and determined by the availability of preferred food types in the context of tolerances within the physical environment. As a first step toward understanding the factors that control *Protoperidinium* spp. populations in natural waters, the distributions of individual *Protoperidinium* species along the southwestern coast of Ireland during the summer of 2003 were characterized, and the relationships between *Protoperidinium* spp. and hydrographic conditions and co-occurring phytoplankton species were examined.

METHOD

Sample collection

From 21–23 July 2003, we sampled seven stations on a north–south transect at 9°17′W in the Celtic Sea (called the "Crease section"), eight stations along a southwest–northeast transect at 51°22′N from offshore to the mouth of Bantry Bay ("Bantry Bay section"), and one station at Fastnet Rock at 51°21′N and 9°45′W between the Celtic Sea and Bantry Bay sections as part of a larger sampling effort along the coast of southern and western Ireland for the Biological Oceanography of Harmful Algal Blooms (BOHAB) project (Fig. 1).

At each station, a SBE 911 CTD was used to obtain hydrographic profiles of temperature, conductivity (salinity), pressure (depth) and fluorescence (chlorophyll) from the surface to 5 m above the bottom. Fluorescence was not calibrated against chlorophyll, but may be used to determine relative levels of chlorophyll in the water. These data were analyzed and plotted using Matlab 7.0.4 software. During the hydrocast at each station, 5 L Niskin bottles were closed at 5–10 discrete depths (surface, 5 m, 10 m, at the chlorophyll maximum layer as determined from a real-time fluorescence profile, and 5–10 m below the chlorophyll maximum) to collect water for plankton community analysis. From each Niskin bottle, 4 L of water was sieved through a 20 μm Nitex sieve. Using <20 μm filtered seawater, the material caught on the sieve was washed into a 15 mL centrifuge tube (Corning 430790, Corning, NY, USA), and the sample was brought to a volume of 14 mL. Samples were preserved with formalin (5% final concentration), and stored at 4°C until analysis.

Plankton counts and species identification

Plankton species were counted in a subset of the sampled stations (six stations along the Crease section, six stations along the Bantry Bay section and one station at Fastnet Rock) using a traditional settling method (Hasle, 1978). The sample was mixed well before 3.7 or 7.4 mL (the equivalent of 1 or 2 L of whole water) was withdrawn by pipette and settled overnight in Hydro-Bios Utermöhl's settling chambers (Campinex, Ltd, Nova Scotia, Canada). To aid in identification of thecate dinoflagellate species, 4 μL of Calcofluor White M2R (Polysciences, Inc., Warrington, PA, USA) at a concentration of 1 mg mL^{-1} was added to the settled sample 1 h prior to counting to stain the cellulose thecal plates of dinoflagellates (Fritz and Triemer, 1985). The entire chamber was counted for *Protoperidinium* spp. at a magnification of ×200 on a Zeiss IM 35 inverted microscope. To enumerate more abundant co-occurring phytoplankton species, multiple diameters or fields were counted at ×200 and formulas applied to determine cell concentrations in cells per liter according to the method of Hasle (Hasle, 1978). All counts were made under tungsten light, switching to

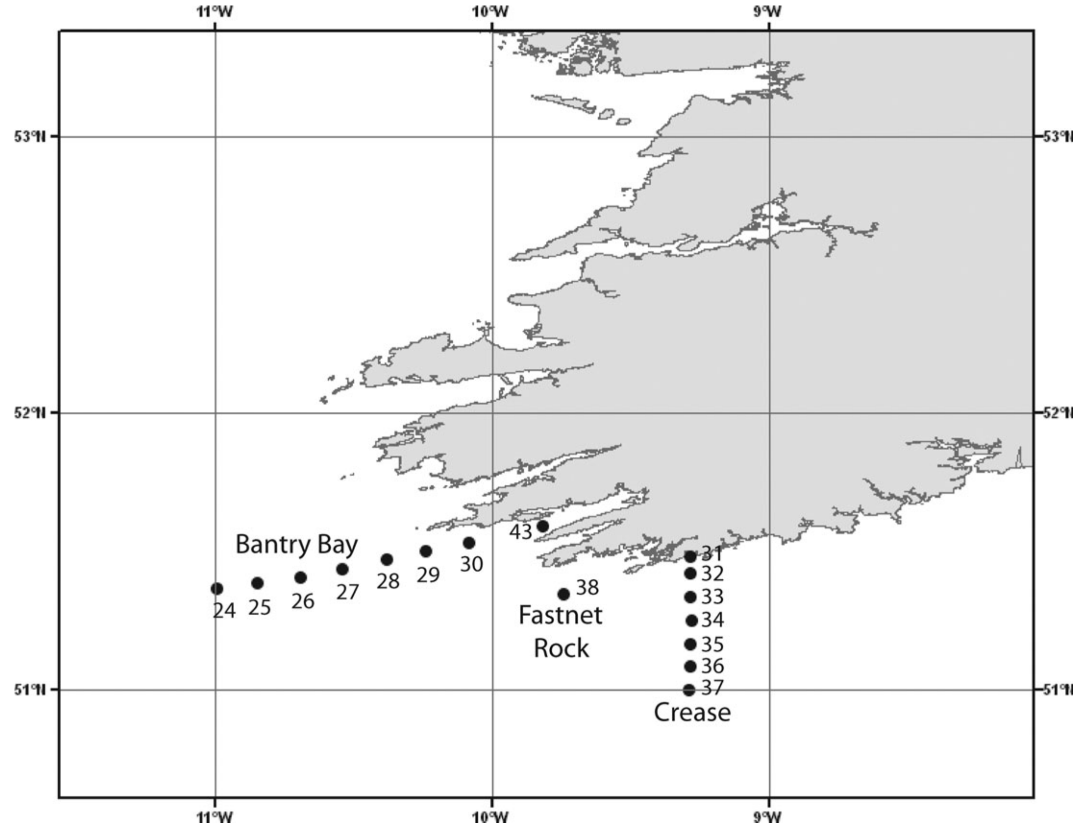


Fig. 1. Map of study area off the coast of southwestern Ireland. Dots show locations of stations sampled.

epifluorescence for dinoflagellate species identification using thecal plate morphology. Replicate counts were not performed. *Protoperidinium* were identified to species level. Species of thecate dinoflagellates other than *Protoperidinium* and diatoms were identified to species or genus level. Athecate dinoflagellates were not well preserved by formalin-fixation, and thus were not counted. Metazoans and protists other than dinoflagellates were categorized into major groups and not identified to genus or species. Species were identified according to Balech (1974), Dodge (1982) and Tomas (1997).

Species relationships

Because many *Protoperidinium* spp. are specific feeders, linear regression was used to find correlations between individual *Protoperidinium* species and individual or groups of phototrophic diatoms and dinoflagellates to determine potential specific predator–prey relationships. The r^2 statistic was used to determine the statistical significance of relationships. Since a particular *Protoperidinium* sp. might be expected to occur only where its preferred prey species was present, but that prey species would not only occur where the predatory *Protoperidinium* sp. was present, those samples, where the given *Protoperidinium* sp. was not detected, were excluded from the analyzes. This method allowed qualitative inference of possible predator–prey relationships, as a positive correlation between the distributions of two species could indicate a predator–prey association. Any relationship found would have to be confirmed by additional laboratory or field studies.

RESULTS

Hydrography

Crease section

The Crease section exhibited well-stratified conditions offshore with more mixed conditions closer to the coast (Fig. 2). Surface to bottom temperatures differed by 6°C, with a distinct thermocline at ca. 25–30 m; a cold sub-thermocline pool was present offshore (Fig. 2A). Colder, less saline and less dense water near the coast, at stations 31 and 32, extending ca. 20 km offshore in

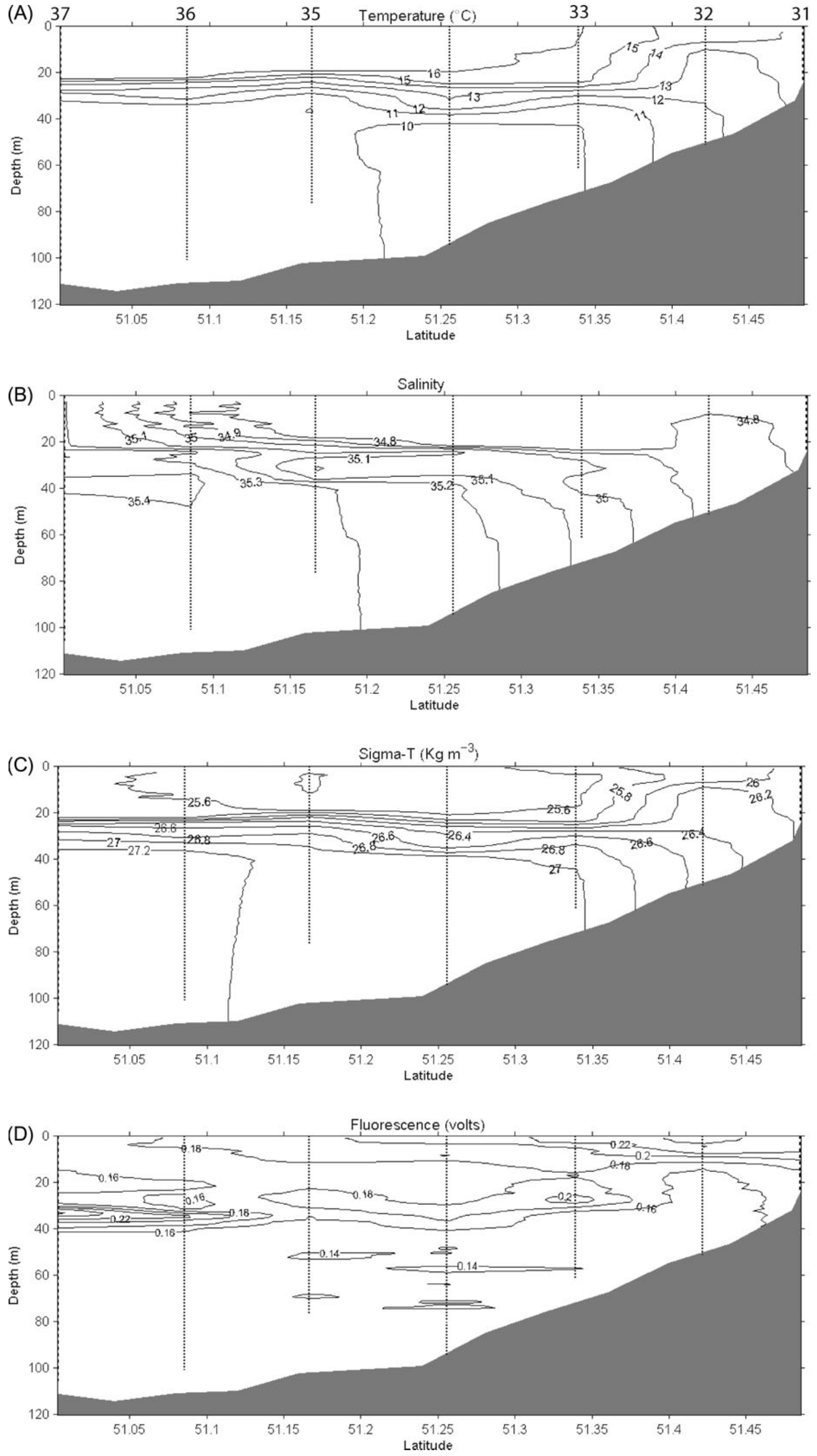


Fig. 2. Cross sectional plots of hydrographic parameters along Crease transect, including (**A**) temperature, (**B**) salinity, (**C**) density and (**D**) relative fluorescence.

the upper 20 m was indicative of a fresh coastal band in the surface waters (Fig. 2B). The Irish Shelf Front was apparent as a strong salinity front separating East North Atlantic Water from the coastal water below the halocline at ca. 51.2°N. Salinity >35.3 typically demarcates this front. The density structure along the Crease section appeared to be dominated by temperature rather than salinity (Fig. 2C). Strong bottom density fronts were evident at ca. 51.4°N, indicating a flow from east to west through this section at that latitude.

Relative fluorescence was measured as a proxy for chlorophyll concentration. Relative fluorescence on the Crease section was generally below 0.18 rfu, but discrete patches of higher fluorescence, near 0.2 rfu, were apparent in the thermocline at 51.35°N and 51.15°N. The highest fluorescence, greater than 0.22 rfu, was seen in discrete patches at the surface nearshore and in the lower portion of the thermocline at the offshore-most stations, between 51°N and 51.1°N.

Fastnet Rock

A single station was sampled at Fastnet Rock, between the Bantry Bay and Crease sections. The temperature, salinity and relative fluorescence profiles for Fastnet Rock are shown in Fig. 3. A strong thermocline was present at 22–28 m, the same depth as the sub-surface maximum in relative fluorescence (ca. 0.2 rfu). The salinity profile shows that, as at the nearshore stations on the Crease section, there was slightly less saline water of 34.8 at the surface, with only a small increase to a salinity of 34.9 at the thermocline and a sharp increase below 60 m to a maximum of >35 at the bottom of the sampled profile at 70 m.

Bantry Bay section

The Bantry Bay section extended from offshore into the mouth of the bay (Fig. 4). Coastal water influence was apparent, particularly at the eastern end of the section. Stratification was well established along the entire transect. As along the Crease section, there was a temperature difference of ca. 6°C between the surface and bottom waters (Fig. 4A). The thermocline was relatively shallow at the mouth of Bantry Bay, at ca. 10 m. Moving west along the transect, the thermocline deepened, narrowing to 25–30 m between 10.2°W and 10.4°W and then widened and further deepened to ca. 30–40 m at 11.0°W. The sub-thermocline pool was slightly warmer than on the Crease section, reflecting the influence of the Shelf Edge Current off the southwest coast.

Salinities were typically 0.1 higher at this location compared to the Crease section (Fig. 4B). Surface and deep waters were freshest at the mouth of Bantry Bay, and salinity increased moving offshore, to greater than 35.5 at depth at the western-most station. The Irish Shelf Front was present as a series of S-shaped isohalines centered on 10.5°W. As on the Crease section, temperature dominated the observed density structure (Fig. 4C). Pronounced bottom fronts were evident at ca. 10.2°W, indicating a geostrophic current flow to the north/northwest on this section. The most offshore station (station 24) on the Bantry section was west of the salinity and density shifts that indicated the Irish Shelf Front.

Patches of high relative fluorescence (0.26 rfu) were evident in the mouth of Bantry Bay, between 9.8°W and 10.1°W, and in discrete patches in the thermocline as the section extended west to the shelf break (0.20–0.22 rfu) (Fig. 4D). At the outermost station, there was a

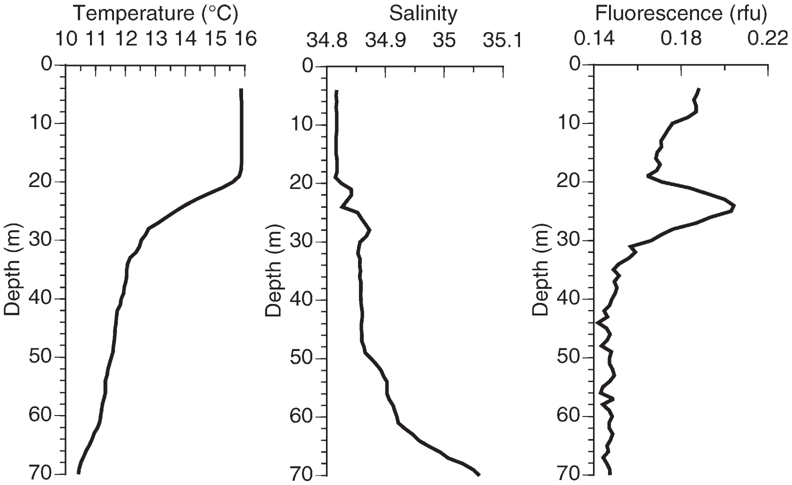


Fig. 3. Profiles of hydrographic parameters at Fastnet Rock station, including temperature, salinity and relative fluorescence.

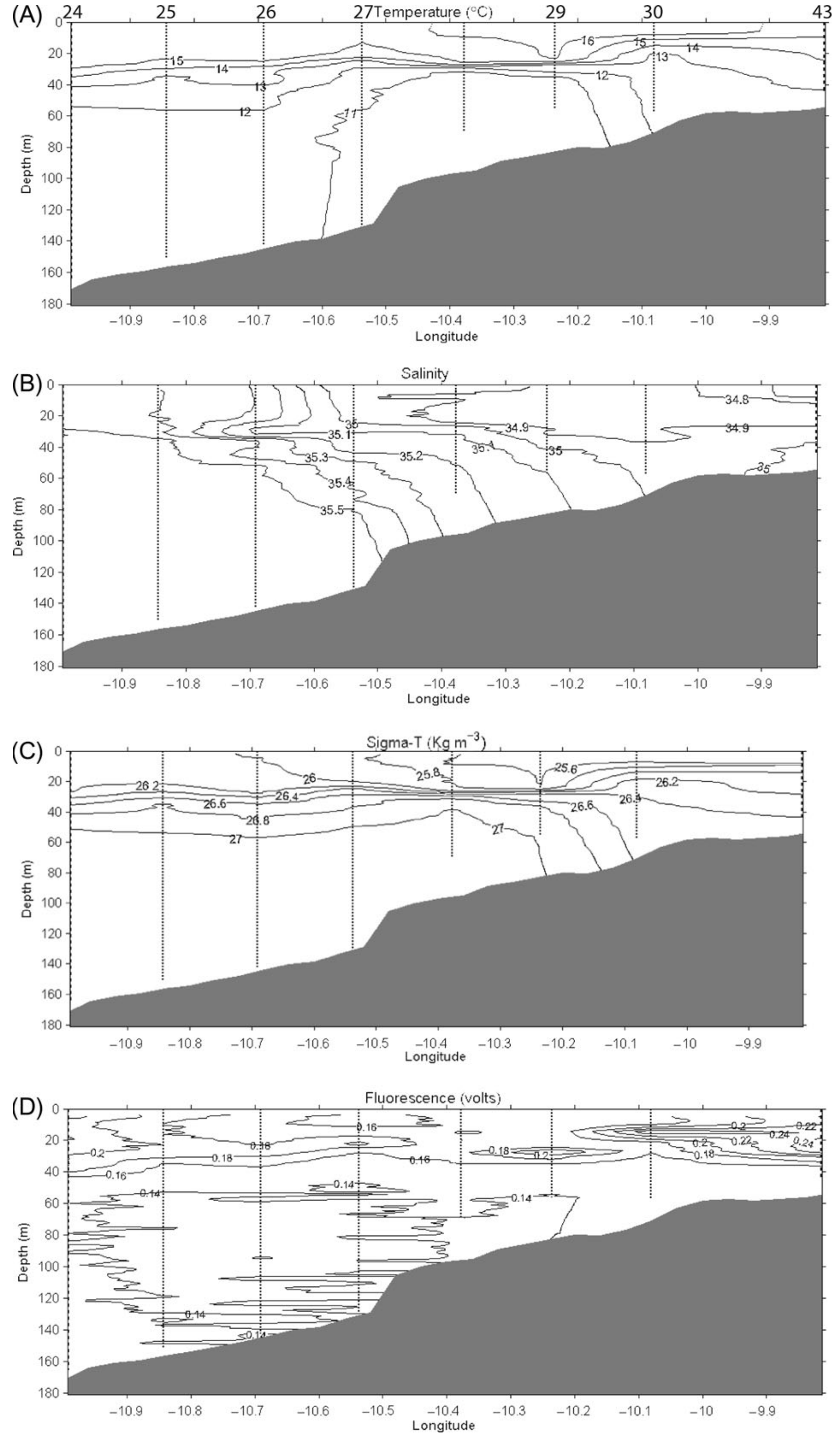


Fig. 4. Cross sectional plots of hydrographic parameters along Bantry Bay transect, including (**A**) temperature, (**B**) salinity, (**C**) density and (**D**) relative fluorescence.

patch of high fluorescence above the thermocline, in the upper 30 m of the water column.

Plankton distributions

Thirty-two species of *Protoperidinium* were identified from the samples analyzed (Table I). A diversity of other dinoflagellate species was present in the study area, with 37 autotrophic or mixotrophic species or genera identified, and 11 species or genera of heterotrophic dinoflagellates other than *Protoperidinium* present (Table II). *Ceratium*, *Dinophysis* and *Prorocentrum* species were among the most abundant phototrophic dinoflagellates. Twenty species or genera of diatoms were found (Table II), with *Rhizosolenia* spp., *Proboscia alata*, *Pseudo-nitzschia* spp. and *Nitzschia* spp., the most abundant and widely distributed.

Crease section

The most offshore station (station 37) on the Crease section, to the south of the Irish Shelf Front, had relatively low concentrations of phytoplankton compared with the rest of the section. North of the Irish Shelf

Table I: Protoperidinium species found in the study area

Protoperidinium achromaticum (Levander) Balech
Protoperidinium bipes (Paulsen) Balech
Protoperidinium brevipes (Paulsen) Balech
Protoperidinium cerasus (Paulsen) Balech
Protoperidinium conicoides (Paulsen) Balech
Protoperidinium conicum (Gran) Balech
Protoperidinium crassipes (Kofoid) Balech
Protoperidinium curvipes (Ostenfeld) Balech
Protoperidinium depressum (Bailey) Balech
Protoperidinium diabolum (Cleve) Balech
Protoperidinium divergens (Ehrenberg) Balech
Protoperidinium excentricum (Paulsen) Balech
Protoperidinium globulum (Stein) Balech
Protoperidinium granii (Ostenfeld) Balech
Protoperidinium leonis (Pavillard) Balech
Protoperidinium marielbourae (Paulsen) Balech
Protoperidinium minutum (Kofoid) Loeblich III
Protoperidinium mite (Pavillard) Balech
Protoperidinium oblongum (Aurivillius) Parke and Dodge
Protoperidinium oceanicum (VanHöffen) Balech
Protoperidinium ovatum Pouchet
Protoperidinium pallidum (Ostenfeld) Balech
Protoperidinium pellucidum Bergh
Protoperidinium pentagonum (Gran) Balech
Protoperidinium punctulatum (Paulsen) Balech
Protoperidinium pyriforme (Paulsen) Balech
Protoperidinium cf. *pyrum* (Balech) Balech
Protoperidinium steinii (Jorgensen) Balech
Protoperidinium subcurvipes (Lebour) Balech
Protoperidinium subinerme (Paulsen) Loeblich III
Protoperidinium thorianum (Paulsen) Balech
Protoperidinium thulense (Balech) Balech

Table II: Plankton species found in the study area, including metazoa

Thecate phototrophic dinoflagellates
- *Alexandrium* sp. Halim
- *Amphidiniopsis* sp. Woloszynska
- *Amphidoma* sp. Stein
- *Amylax* sp. Meunier
- *Ceratium furca* (Ehrenberg) Claparède and Lachmann
- *Ceratium fusus* (Ehrenberg) Dujardin
- *Ceratium hexicantum* Gourret
- *Ceratium horridum* (Cleve) Gran
- *Ceratium lineatum* (Ehrenberg) Cleve
- *Ceratium longipes* (Bailey) Gran
- *Ceratium macroceros* (Ehrenberg) Cleve
- *Ceratium minutum* Jorgensen
- *Ceratium setaceum* Jorgensen
- *Ceratium trichoceros* (Ehrenberg) Kofoid
- *Ceratium tripos* (O.F. Müller) Nitzsch
- *Corythodinium* sp. Lobelich Jr. and Loeblich III
- *Dinophysis acuminata* Claparède and Lachmann
- *Dinophysis acuta* Ehrenberg
- *Dinophysis dens* Pavillard
- *Dinophysis naustum* (Stein) Parke and Dixon
- *Dinophysis norvegica* Claparède and Lachmann
- *Dinophysis ovum* Schutt
- *Dinophysis punctata* Jorgensen
- *Dinophysis rotundata* Claparède and Lachmann
- *Dinophysis* sp. Ehrenberg
- *Dinophysis tripos* Gourret
- *Gonyaulax* sp. Diesing
- *Gymnodinium* sp. Stein
- *Lingulodinium polyedrum* (Stein) Dodge
- *Podolampas palmipes* Stein
- *Prorocentrum gracile* Schütt
- *Prorocentrum micans* Ehrenberg
- *Prorocentrum* sp. Ehrenberg
- *Pyrocystis lunula* (Schütt) Schütt
- *Scrippsiella* sp. Balech ex Loeblich III
- *Triadinium polyedricum* (Pouchet) Dodge

Thecate heterotrophic dinoflagellates
- *Diplopsalis lenticula* Bergh
- *Diplopsalis* sp. Bergh
- *Dissodinium* sp. Abé
- *Dissodium asymmetricum* (Magin) Lobelich
- *Noctiluca scintillans* (Macartney) Kofoid and Swezy
- *Oblea rotunda* (Lebour) Balech ex Sournia
- *Preperidinium lenticulatum* (syn. *Zygabikodinium lenticula*) (Pavillard) Elbrächter
- *Preperidinium* sp. Mangin
- *Pronoctiluca* sp. Fabre-Domergue
- *Pyrocystis lunula* (Schütt) Schütt

Diatoms
- *Asterionella* sp. Hassall
- Centric diatom spp.
- *Chaetoceros* spp. Ehrenberg
- *Coscinodiscus* spp. (Ehrenberg) Hasle and Sims
- *Leptocylindrus danicus* Cleve
- *Leptocylindrus mediterraneum* (H. Peragallo) Hasle
- *Leptocylindrus* sp. Cleve
- *Melosira* sp. C.A. Agardh
- *Navicula* sp. Bory
- *Nitzschia* spp.
- *Paralia sulcata* (Ehrenberg) Cleve
- Pennate diatom spp.
- *Proboscia alata* (Brightwell) Sudström
- *Pseudoguinardia* sp. von Stoch
- *Pseudo-nitzschia* spp.

Continued

Table II: Continued

Rhizosolenia spp. Brightwell
Rhizosolenia delicatula Cleve
Skeletonema sp. Greville
Thalassiosira sp. (Cleve) Hasle
Chromophytes
Halosphaera parkeae Boalch and Mommaerts
Metazoa
Copepods
Copepod nauplii
Larve
Other protists
Ciliates
Coccolithophorids
Dictyocha spp.
Foraminifera
Radiolaria
Tintinnids

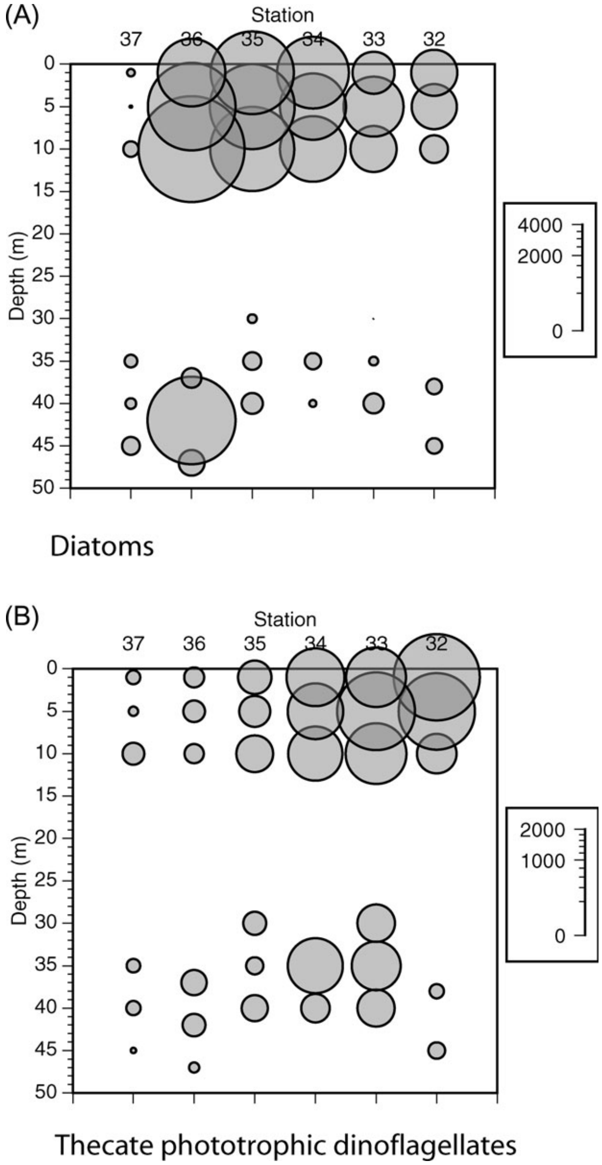
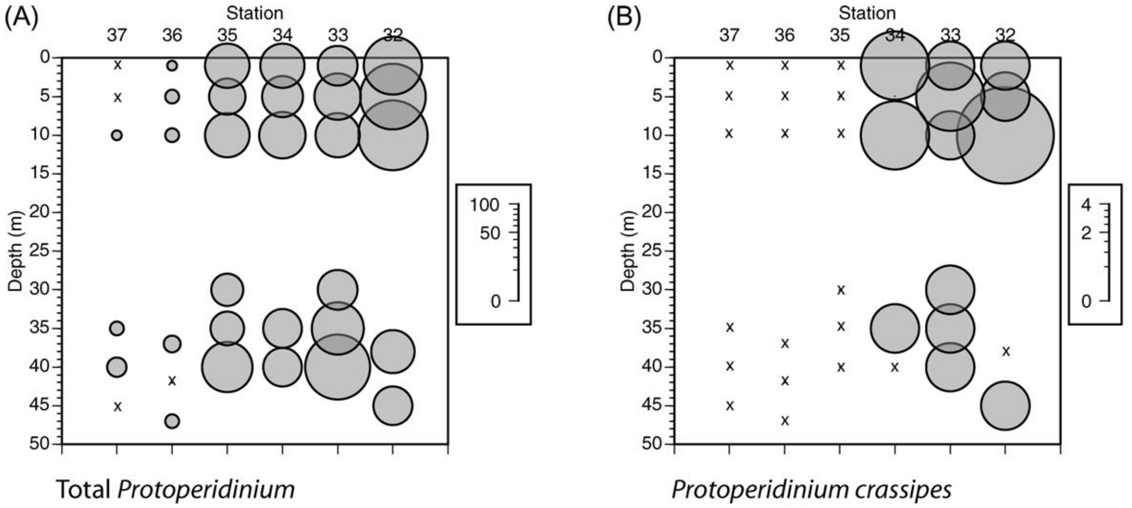


Fig. 5. Concentrations along Crease section in cells per liter of (**A**) total diatoms and (**B**) total thecate phototrophic dinoflagellates.

Front, the plankton community was dominated by diatoms in the offshore stratified surface waters (Fig. 5A), but transitioned to a dinoflagellate-dominated community (Fig. 5B) in the area of upwelling inshore. The deep offshore fluorescence maximum on the Crease section (Fig. 2D) was likely due to picoplankton, as large phototrophs were in low abundance at this station, relative to the rest of the section. The concentration of total diatoms along the Crease section was largely determined by the abundance of the dominant diatom species, *Proboscia alata*. Concentrations of *P. alata* were generally highest in the surface waters and increased from nearshore to offshore, exclusive of station 37. At station 36, a high concentration of *P. alata* (2689 cells L^{-1}) was found at a depth of 42 m, well below the thermocline.

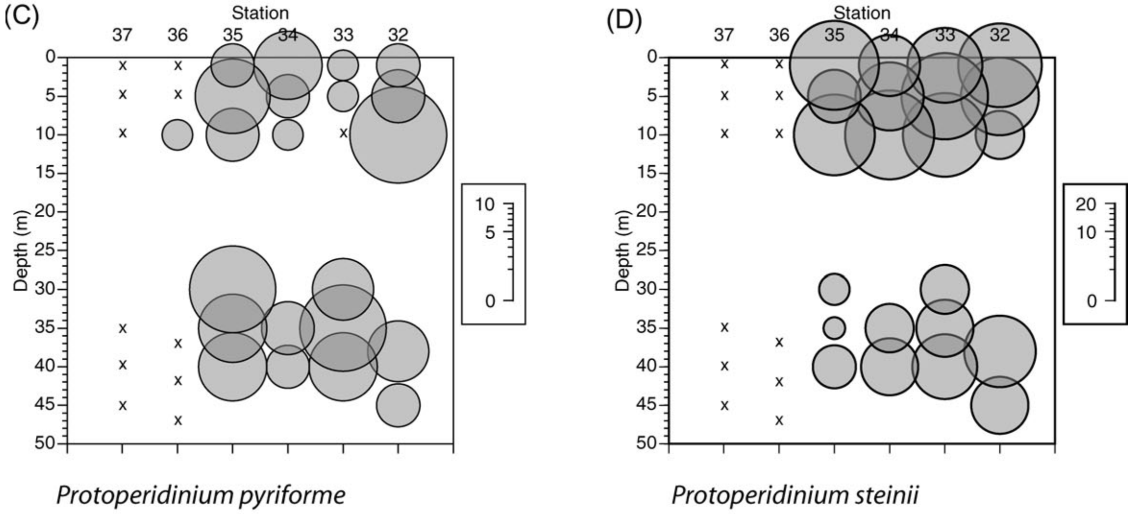
In contrast to the distribution of diatoms, total phototrophic thecate dinoflagellates were more abundant nearshore and decreased moving south and offshore along the transect (Fig. 5B). Phototrophic dinoflagellates were most abundant in the surface waters, but were also present at depths near the thermocline at stations in the middle of the transect. The dinoflagellate community along the Crease section was dominated by *D. acuta*, *C. lineatum*, and *Prorocentrum* spp. *Dinophysis acuta* was most abundant nearshore and at the surface, with a maximum concentration of 645 cells L^{-1}. *Ceratium lineatum* was most abundant at the nearshore stations, primarily in the surface waters, although high concentrations were found at depth at stations 33 and 34, in the layer of highest fluorescence, with a maximum of 306 cells L^{-1} at 35 m. Concentrations of *Prorocentrum* spp. were highest in the surface waters, particularly at the nearshore stations.

Concentrations of total *Protoperidinium* spp. were highest nearshore, low in the two most southern and offshore stations, and distributed through the water column at the most inshore stations (Fig. 6A). *Protoperidinium crassipes* was not detected in the offshore waters, and appeared confined to the nearshore stations along the Crease section at concentrations never exceeding 4 cells L^{-1} (Fig. 6B). *Protoperidinium pyriforme* was distributed throughout the water column at concentrations below 10 cells L^{-1} at the nearshore stations (Fig. 6C). Similarly, *P. steinii* was found only at the nearshore stations, but was in slightly higher concentrations in the surface waters than deep, with a maximum concentration of 17 cells L^{-1} (Fig. 6D). In contrast, *P. depressum* was limited primarily to deeper waters at or



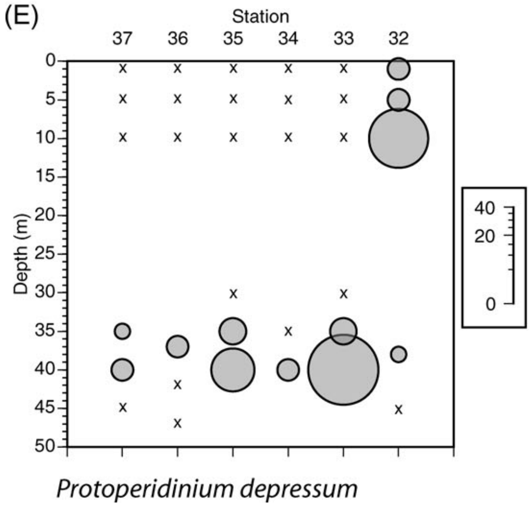
Total *Protoperidinium*

Protoperidinium crassipes



Protoperidinium pyriforme

Protoperidinium steinii



Protoperidinium depressum

Fig. 6. Concentrations of *Protoperidinium* spp. along Crease section in cells per liter; x indicates not detected: (**A**) total *Protoperidinium*, (**B**) *P. crassipes*, (**C**) *P. pyriforme*, (**D**) *P. steinii* and (**E**) *P. depressum*.

below the thermocline, and was only found in surface waters at the nearshore station. Concentrations of *P. depressum* did not exceed 25 cells L^{-1} in any sample (Fig. 6E).

Fastnet Rock

There were relatively high concentrations of both diatoms and dinoflagellates at the Fastnet Rock station. The concentration of total diatoms was highest in surface waters, with a maximum concentration of more than 3450 cells L^{-1} at a depth of 5 m (Fig. 7A). Total diatoms were slightly less abundant at the chlorophyll maximum, with 2300 cells L^{-1} at 25 m, and dropped to 450 cells L^{-1} at 30 m.

As on the Crease section, the profiles of individual diatom species diverged from that of total diatoms. *Proboscia alata* was the most abundant diatom at Fastnet Rock, and dictated the concentration of total diatoms in the surface waters, with over 3400 cells L^{-1} at 5 m. All other prevalent diatom species had their highest concentrations at depth. *Pseudo-nitzschia* spp., *Rhizosolenia* spp. and *Navicula* spp. were all at highest concentration at 25 m, corresponding with the thermocline and the maximum in fluorescence. The concentration of *Leptocylindrus* spp. was highest at the thermocline, near 70 cells L^{-1} at both 25 and 31 m.

The concentration of total phototrophic dinoflagellate species at Fastnet Rock increased from the surface to the thermocline, with 300 cells L^{-1} in the surface waters and a concentration of more than 1000 cells L^{-1} at a depth of 25 m (Fig. 7B). At 30 m, the concentration of total phototrophic dinoflagellates was less than 40 cells L^{-1}. *Dinophysis acuta* and *C. lineatum* were the most abundant thecate phototrophic dinoflagellates species, with concentrations increasing with depth to maximums at 25 m of 386 and 480 cells L^{-1}, respectively. *Dinophysis acuminata* cell concentrations also increased with depth to 25 m, with a maximum of 33 cells L^{-1}. Conversely, *Prorocentrum* spp., composed primarily of *P. micans*, reached maximum concentrations above the thermocline, reaching 184 cells L^{-1} at 10 m.

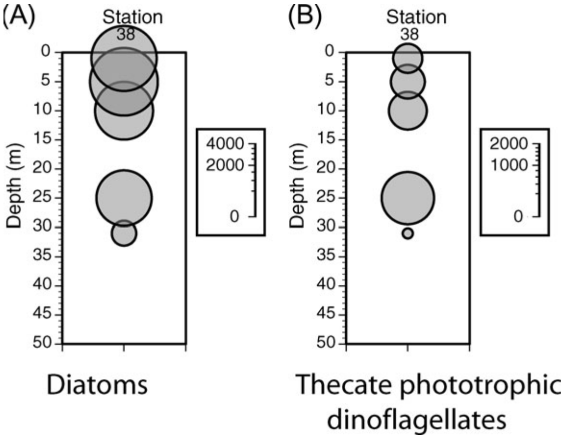


Fig. 7. Concentrations at Fastnet Rock station in cells per liter of (**A**) total diatoms and (**B**) total thecate phototrophic dinoflagellates.

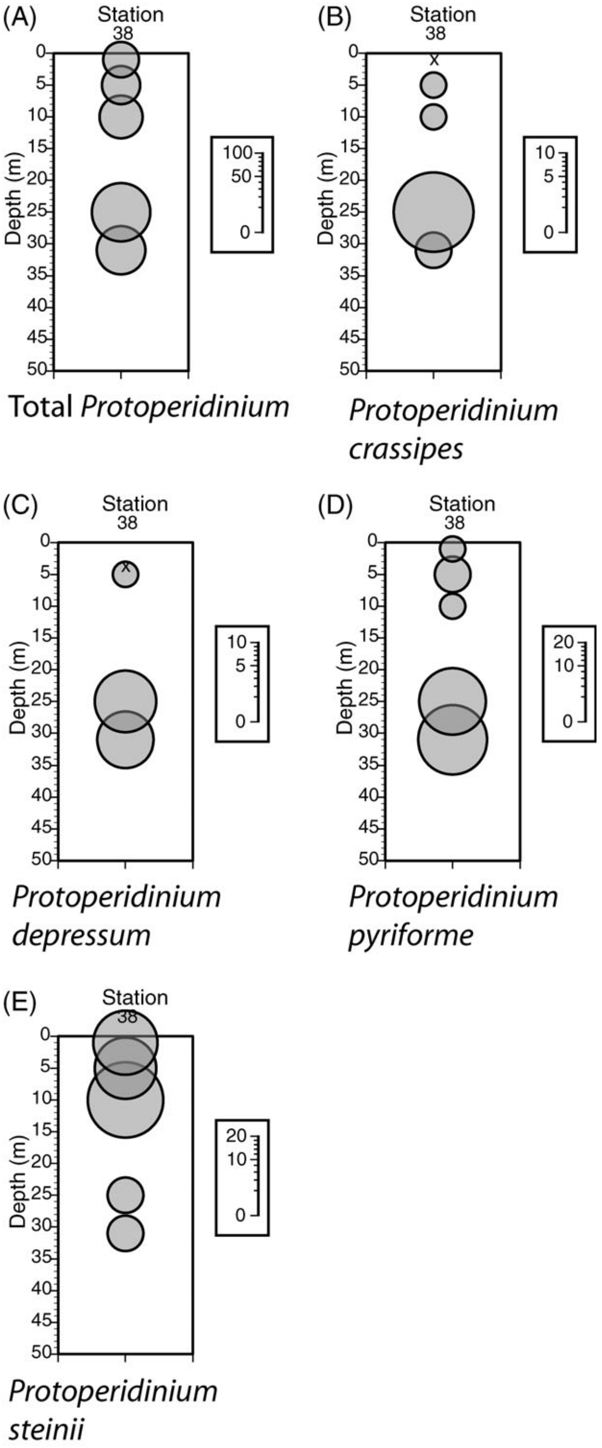
Protoperidinium spp. had a low relative abundance, compared with other dinoflagellates and with diatoms. Concentrations of total *Protoperidinium* spp. at Fastnet Rock were highest at 25 m (54 cells L^{-1}) and were elevated below the thermocline compared with the surface waters (Fig. 8A). Although *P. crassipes* (Fig. 8B), *P. depressum* (Fig. 8C) and *P. pyriforme* (Fig. 8D) all reached their highest abundances (from 6–15 cells L^{-1}) at 25 or 31 m, *P. steinii* (Fig. 8E) was most abundant in the surface waters, with a maximum concentration of 18 cells L^{-1} at 10 m.

Bantry Bay section

The Bantry Bay transect had higher concentrations of both diatoms and dinoflagellates than did either the Crease section or Fastnet Rock. Total diatom abundances were highest in the mouth of the bay with a maximum of ca. 53 300 cells L^{-1} at 1 m depth, and at the offshore-most station where the maximum concentration was ca. 46 800 cells L^{-1}, with lower concentrations along the center of the section (Fig. 9A). The diatom community nearshore was dominated by *Proboscia alata*, *Pseudo-nitzschia* spp., *Rhizosolenia* spp. and *Leptocylindrus* spp. At the western-most station, those genera were nearly absent, and small *Nitzschia* spp. dominated the community, reaching a maximum concentration of ca. 53 200 cells L^{-1}.

The dinoflagellate community along the Bantry Bay section was more diverse than on the Crease section or at the Fastnet Rock station. The concentration of total phototrophic dinoflagellates were highest in the mouth of Bantry Bay with a peak concentration of more than 17 000 cells L^{-1} at a depth of 27 m (Fig. 9B), and was comprised largely by the most abundant species, *C. setaceum*, *C. fusus* and *Prorocentrum* spp.

As expected, different dinoflagellate species, even those of the same genus, had varying distributions along the transect. Within the most abundant genus, *Ceratium*, *C. fusus* and *C. setaceum* had similar distributions—low to non-detectable at all stations except in the mouth of Bantry Bay, with the highest concentrations at 27 m. *Ceratium lineatum* was not detectable in the mouth of Bantry Bay, and was most abundant at 10 m along the middle of the section (500 cells L^{-1}), whereas *Ceratium tripos* was not seen in the nearshore stations and was distributed through the water column at the outermost station. Seven different species of *Dinophysis* were present



Total *Protoperidinium*

Protoperidinium crassipes

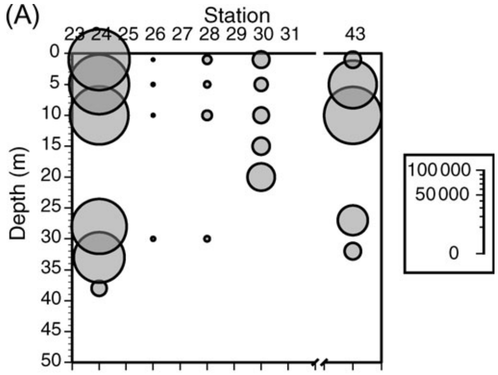
Protoperidinium depressum

Protoperidinium pyriforme

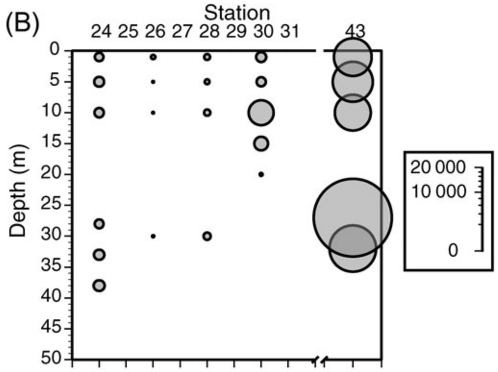
Protoperidinium steinii

Fig. 8. Concentrations of *Protoperidinium* spp. at Fastnet Rock station in cells per liter; x indicates not detected: (**A**) total *Protoperidinium*, (**B**) *P. crassipes*, (**C**) *P. depressum*, (**D**) *P. pyriforme* and (**E**) *P. steinii*.

along the Bantry Bay section, with *D. acuminata* and *D. acuta* being most abundant. *Dinophysis acuminata* was found primarily in the mouth of Bantry Bay, distributed through the water column at concentrations near 100 cells L^{-1}. *Dinophysis acuta* was detected from the mouth of Bantry Bay to the center of the section, with a



Diatoms



Thecate phototrophic dinoflagellates

Fig. 9. Concentrations of diatoms along Bantry Bay section in cells per liter of (**A**) total diatoms and (**B**) total thecate phototrophic dinoflagellates.

maximum concentration of 885 cells L^{-1} at 10 m depth at station 30. *Prorocentrum micans* was located predominantly in the surface waters at the mouth of Bantry Bay (ca. 2400 cells L^{-1} at 5 m). Relatively high concentrations of *Scrippsiella* were found only in the surface waters at the mouth of Bantry Bay (1000 cells L^{-1} at 5 m).

The concentration of total *Protoperidinium* spp. was highest in the mouth of Bantry Bay (maximum 561 cells L^{-1} at 27 m), about half as high at the most offshore station (201 cells L^{-1} at 33 m) and low in between (Fig. 10A). *Protoperidinium* spp. were distributed through the water column. A few species were found in low concentrations across the entire section, but most *Protoperidinium* spp. were located either primarily near the mouth of Bantry Bay, or primarily at the offshore-most station. At the mouth of the bay, *P. steinii* (maximum 190 cells L^{-1} at 32 m) (Fig. 10B), *P. minutum* (maximum 119 cells L^{-1} at 27 m) (Fig. 10C), *P. mite* (99 cells L^{-1} at 33 m) (Fig. 10D) and *P. pyriforme* (maximum 35 cells L^{-1} at 32 m) (Fig. 10E) were most abundant below the thermocline, whereas *P. pellucidum* (maximum 171 cells L^{-1} at 1 m) (Fig. 10F) and *P. brevipes* (maximum 123 cells L^{-1} at 10 m) (Fig. 10G) were found in the surface waters. *Protoperidinium punctulatum* (Fig. 10H) and *P. depressum* (Fig. 10I) were found at the mouth of Bantry Bay through the whole water column, but in concentrations below 20 cells L^{-1}. *Protoperidinium crassipes* (Fig. 10J) was distributed sparsely across the section and had its highest abundance of any station on the survey at the offshore-most station where it was found through the water column with a maximum concentration of 38 cells L^{-1} at 5 m.

To investigate possible specific predator–prey relationships between *Protoperidinium* species and individual species or groups of phytoplankton, regression analyzes were conducted on concentrations of individual *Protoperidinium* spp. and individual or groups of diatom or dinoflagellate species. Most species pairs did not have statistically significant positive correlations or were negatively correlated.

DISCUSSION

Many informative studies of phytoplankton distribution and hydrography along the southwest coast of Ireland have been conducted in the past (e.g. Raine *et al.*, 1990, 1993, 2001, 2002; McMahon *et al.*, 1995, 1998; Raine and McMahon, 1998; Fernand *et al.*, 2006), but little detailed information was available about the distributions of *Protoperidinium* spp. in the area. The current study begins to define the ecologies of individual *Protoperidinium* species and co-occurring phytoplankton prey in the context of the hydrography of the region. These results may be used to estimate the potential trophic impact of *Protoperidinium* in southwestern Ireland during the late summer.

Hydrography and plankton distributions

Physically defined boundaries, like thermoclines and fronts, can be important for determining plankton populations inside the bays along the southwestern coast of Ireland. As in previous studies, we found geostrophic flows to the west along the southern coast of Ireland, wrapping around and flowing north/northwest past the mouth of Bantry Bay (Raine *et al.*, 1990, 1993, 2001; Dodge, 1994; McMahon *et al.*, 1995, 1998; Raine, 1996; McMahon *et al.*, 1998; Raine and McMahon, 1998; Fernand *et al.*, 2006). The normal mid-summer flow in this region inshore of the front is clockwise around the coast, whereas offshore of the Irish Shelf

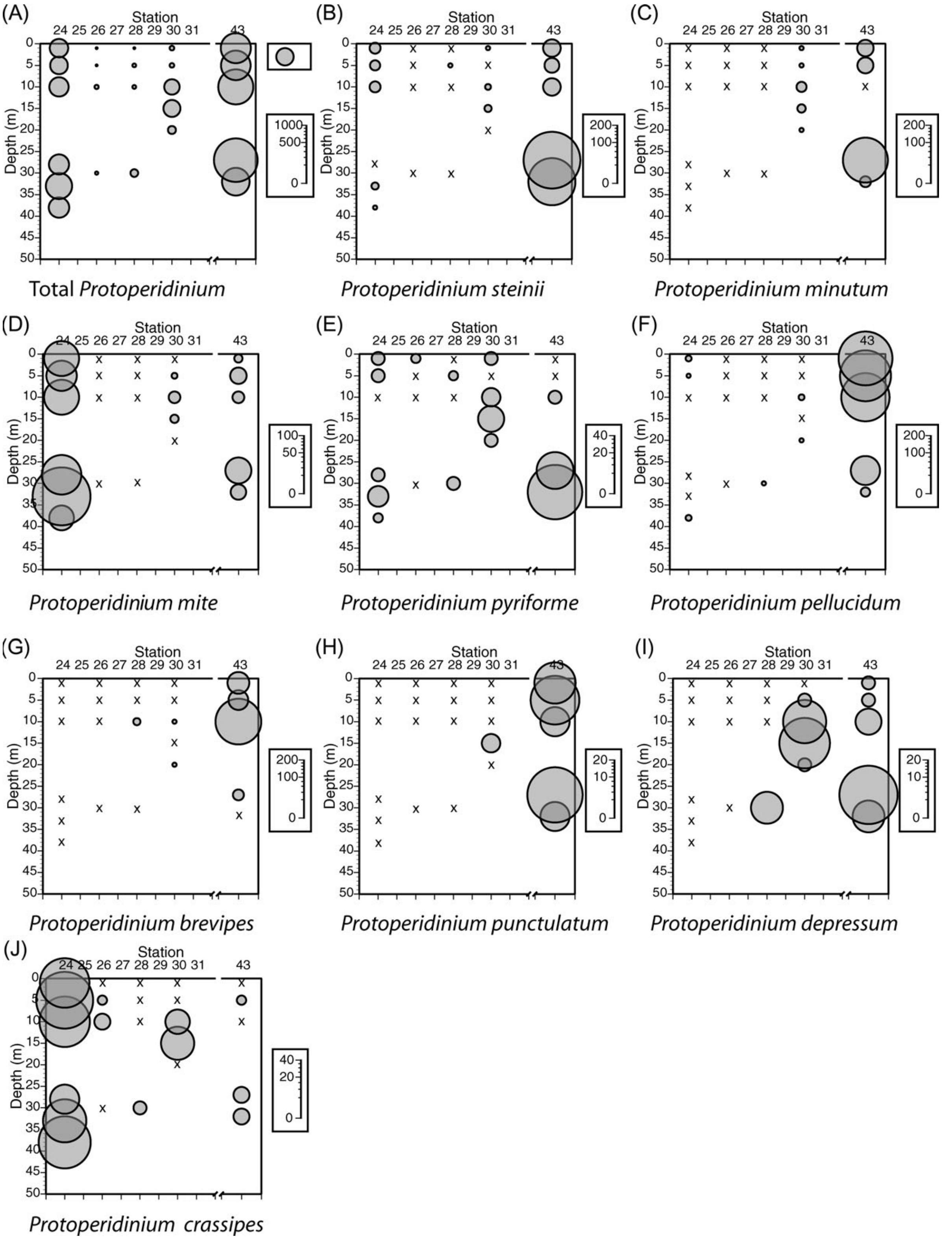


Fig. 10. Concentrations of *Protoperidinium* spp. along Bantry Bay section in cells per liter; x indicates not detected: (**A**) total *Protoperidinium*, (**B**) *P. steinii*, (**C**) *P. minutum*, (**D**) *P. mite*, (**E**) *P. pyriforme*, (**F**) *P. pellucidum*, (**G**) *P. brevipes*, (**H**) *P. punctulatum*, (**I**) *P. depressum* and (**J**) *P. crassipes*.

Front the flow is toward the south (Raine and McMahon, 1998; Fernand *et al.*, 2006). Thus, plankton populations that form nearshore and are concentrated along the thermocline in the Celtic Sea have the potential to be entrained and transported to the northwest along the coast, past the large southwestern bays. With southwesterly winds, these populations can be transported into the bays and deposited there when the winds relax (Raine *et al.*, 1993; Edwards *et al.*, 1996; Raine and McMahon, 1998). Through this transport and with appropriate growth conditions, blooms can form very rapidly in the southwestern bays. Offshore monitoring of plankton abundances and distributions, when combined with observations of wind and weather conditions, could allow predictions of plankton blooms in southwestern bays and be used to determine the potential for impact of toxic or harmful phytoplankton species on shellfish and finfish aquaculture in bays. At the time of sampling, the highest concentrations of the putative AZA toxin producer, *P. crassipes*, occurred offshore of Bantry Bay, well away from sites of shellfish aquaculture. During this same time period, no AZA was detected in shellfish in southwestern Ireland. These results unfortunately do not allow determination of whether *P. crassipes* is responsible for AZA toxicity in the region.

The Irish Shelf Front is a well-characterized feature off the southern and southwestern coasts of Ireland, and during this survey was located in the same general region in the Celtic Sea and west of Bantry Bay as in previous studies (Huang *et al.*, 1991; McMahon *et al.*, 1995; Raine and McMahon, 1998). On both the Crease and Bantry Bay sections, the plankton community differed across the front. On the Crease section, phytoplankton and heterotrophic dinoflagellates were more abundant and more diverse inshore of the Irish Shelf Front than offshore and to the south of the front. Along the Bantry Bay transect, diatoms were more abundant offshore, whereas dinoflagellates had their highest concentrations inshore, with substantial variability in distributions between species. Although the distributions of phytoplankton and *Protoperidinium* appeared to be related to the location of the Irish Shelf Front, the salinity range in the study area was too narrow to accurately test salinity tolerances for individual species of *Protoperidinium*.

In this study, diatoms dominated in the stratified waters offshore, whereas dinoflagellates dominated in the nearshore, better-mixed waters on the Crease section. One might have expected, and indeed, previous studies in this region have found, that diatoms fare better in turbulent or well-mixed waters, whereas dinoflagellates dominate in stratified waters (McMahon *et al.*, 1995). In this case, the strong fresh water influence in the surface waters nearshore may have contributed to the higher relative abundance of dinoflagellates possibly by stabilizing the water column or promoting higher growth rates (Franks and Anderson, 1992). The diatom community offshore was dominated by *Proboscia alata*, a species known to bloom in the summer, in relatively low nutrient conditions, in contrast to "typical" diatoms (Lange *et al.*, 1992; Sukhanova *et al.*, 2006).

The *Protoperidinium* species detected in this study may be broadly categorized into three groups (widespread, nearshore and offshore) based on their differential geographic distributions in the survey region, perhaps indicating similarities in environmental and prey requirements of the species within each group. The majority of *Protoperidinium* species were widespread during the time of the survey. Several species, including *P. bipes*, *P. achromaticum*, *P. granii*, *P. leonis*, *P. marielebourae*, *P. subinerme*, *P. thulense*, *P. pentagonum* and *P. thorianum*, were found only inshore of the Irish Shelf Front. Only *P. oceanicum* was found exclusively offshore of the front.

These groupings correspond very well with those determined by the cluster analysis of Dodge for *Protoperidinium* species in a study of the larger area of the Northeastern Atlantic, from northern Africa to the North Sea (Dodge, 1994), with relatively few exceptions. Those species listed by Dodge as having a "neritic distribution" were the same as those found only inshore of the Irish Shelf Front in the current study, with the exceptions of *P. leonis* and *P. subinerme*, which Dodge found to be widespread, and *P. bipes*, which was not included in the earlier study. Similarly, the species found to be widespread in the current study were included in Dodge's "common" or "middle-latitudes or widespread" clusters. None of the "warm water" species found by Dodge in waters to the south of the British Isles were found in this study. This suggests that the associations of these *Protoperidinium* species are relevant over the long term and on both the large spatial scales explored in previous studies (Dodge, 1994) and on smaller spatial scales like that of the present study.

Current patterns appear to play a role in the geographic distribution of *Protoperidinium* species. All of the *Protoperidinium* species found at the Fastnet Rock station were also found along both the Celtic Sea and Bantry Bay sections. Both *P. bipes* and *P. thorianum*, found only inshore of the Irish Shelf Front on the Bantry and Celtic Sea sections, were also found at the Fastnet Rock station, suggesting that nearshore *Protoperidinium* populations were connected between Bantry Bay and the Celtic Sea by the prevailing northwestward currents inshore of the Irish Shelf Front. A single species, *P. thulense*, was found on the Celtic Sea section, but not on the Bantry Bay section. Several species were exclusive to the Bantry Bay section, however, including *P. conicum*, *P. granii*, *P. leonis*, *P. mite*, *P. oblongum*, *P. pentagonum* and *P. subinerme*. These species may be blocked from dispersal to the southeast of Bantry Bay by the northwestward currents.

Along both transects, the highest phytoplankton and *Protoperidinium* concentrations often occurred at the thermocline, a phenomenon seen previously in this region (Raine *et al*., 1990, 1993; Raine and McMahon, 1998; Cusack *et al*., 2006). Elevated densities of plankton are often found at such physical discontinuities. Temperature dictated the density structure along the southwest coast of Ireland during the time of the study, so the thermocline corresponds with the pycnocline, and may be a region of accumulation. Alternatively, the cells within the thermocline may be striking a balance between access to light near the surface and nutrients and prey available in deeper waters, as the stratified surface waters become nutrient-depleted over the summer. The range in temperature was too narrow, and concentrations of *Protoperidinium* spp. were too low, to accurately resolve temperature tolerance windows for individual species.

Protoperidinium–phytoplankton relationships

Although *Protoperidinium* might be expected to be found with its phytoplankton prey, chlorophyll fluorescence was not a good predictor of the distribution of a given *Protoperidinium* species over the large, heterogeneous area of the survey. Relative fluorescence is generally considered a reliable indicator of chlorophyll concentration, but does not discriminate between different sources of primary productivity, such as picoplankton versus large diatoms. In the mouth of Bantry Bay, at stations 30 and 43, for example, a maximum in fluorescence existed at a depth of 15–20 m. No corresponding maximum in total diatoms or total dinoflagellates is seen at this depth compared with other areas with lower fluorescence along the transect. The deep fluorescence maximum here was likely caused by picoplankton too small to be detected by our sampling methods. On the other hand, a peak in total diatom cell concentration matched the fluorescence maximum at station 24 to the west of the Irish Shelf Front. Such differences in the primary producers at the base of the food chain would lead to very different plankton community structures, like the difference between the offshore and nearshore *Protoperidinium* species seen in this study. Cyanobacteria and picoeukaryotes, although important for the ecology of the system, may be ignored for the purposes of the trophic ecology of *Protoperidinium*, since *Protoperidinium* thus far have been shown to have positive growth rates only on planktonic prey of their own size (Jacobson and Anderson, 1986; Jeong and Latz, 1994; Buskey, 1997; Naustvoll, 2000; Menden-Deuer, *et al*., 2005).

Few statistically significant correlations between individual *Protoperidinium* species and specific phototrophs were found, likely due in part to the high degree of variability in cell concentrations and relatively low concentrations of most *Protoperidinium* species in the study area. There are a number of possible explanations for a lack of significant correlations between *Protoperidinium* and putative specific prey species in the field. First, there may be a time lag between the peak concentrations of prey and predator, as might be expected in a zooplankton–phytoplankton predator–prey relationship. This would not have been detected in our single time point study. Sampling over time would help to clarify possible species-specific relationships. Second, the distribution of *Protoperidinium* species was likely determined in part by predation by larvae and other mesozooplankton, organisms not quantified in this study. Third, *Protoperidinium* species may have preferred food types, as has been demonstrated for some species in the laboratory, but likely supplement their diets with additional species, leading to less-than-perfect correlations in the field. Some *Protoperidinium* species may prey on organisms normally thought to belong to higher trophic levels. *Protoperidinium* cf. *divergens* has been shown to consume copepod eggs and nauplii, for example (Jeong, 1996). Finally, some *Protoperidinium* spp. have been shown to survive for extended periods of time, up to 71 days in the case of *P. depressum*, in conditions of starvation or extremely low food availability (Jakobsen and Hansen, 1997; Menden-Deuer *et al*., 2005). The ability to endure extended starvation is a useful strategy for a planktonic predator, particularly one that is a specific feeder on patchy or limited food resources. Thus, the presence of a *Protoperidinium* species in an area does not guarantee that conditions there were optimal for growth.

Protoperidinium and other microzooplankton may play an important role in control of phytoplankton populations. In the waters off the southwestern coast of Ireland at the time of this study, *Protoperidinium* spp. were likely competing with other consumers of large phytoplankton, including copepods and other heterotrophic dinoflagellates, particularly *Noctiluca scintillans*, which was abundant (data not shown). Growing evidence indicates that the impact of microzooplankton like *Protoperidinium* on phytoplankton populations, bloom structure and cycling of organic matter can be important—even more significant than that of mesozooplankton—at particular times and locations (Smetacek, 1981; Archer *et al*., 1996; Tiselius and Kuylenstierna, 1996; Tillmann and Hesse, 1998; Kjaeret *et al.*, 2000; Fileman and Burkill, 2001; Levinsen and Nielsen, 2002; Verity *et al.*, 2002). Few authors have attempted evaluations of grazing impact of individual or groups of *Protoperidinium* species in the field, however. Grazing rates have been measured in the laboratory for only a few thecate heterotrophic dinoflagellate species feeding on selected prey, and vary among species and prey types, making it difficult to extrapolate results of laboratory grazing studies to the field. These limited measurements are still useful, however, in that they can help estimate the potential trophic impact of *Protoperidinium* species in the field.

Protoperidinium pellucidum, for example, has a maximum ingestion rate of 0.78 prey cells dinoflagellate^{-1} h^{-1} (Buskey, 1997) when feeding on the diatom *D. brightwellii*. With a maximum concentration of 170 cells L^{-1} at the mouth of Bantry Bay, *P. pellucidium* could consume ~80% of the standing stock of total diatoms per day at the same station, assuming a constant grazing rate on all diatom species. At the other end of the grazing spectrum, *P. crassipes* has one of the lowest reported grazing rates, consuming 0.1 prey cells dinoflagellate^{-1} h^{-1} when feeding on the dinoflagellate *L. polyedrum* (Jeong and Latz, 1994). *Protoperidinium crassipes* was found in low concentration in the study area, with a maximum concentration of 38 cells L^{-1} offshore on the Bantry Bay section. Phototrophic dinoflagellates are the preferred prey of *P. crassipes* (Jeong and Latz, 1994), so if this low grazing rate were constant in the field, *P. crassipes* could consume 30% of the standing stock of phototrophic dinoflagellates per day offshore. As these estimates of grazing are for single *Protoperidinium* species, the trophic impact of thecate heterotrophic dinoflagellates in the waters of southwestern Ireland may be even higher. Phytoplankton community composition and environmental conditions such as temperature may influence grazing rates of *Protoperidinium* species in the field, however. Quantification of the trophic role of *Protoperidinium* in different environments is needed, and may help determine if *Protoperidinium* are important as vectors of phycotoxins.

CONCLUSIONS

This study investigated the diversity and biogeography of *Protoperidinium* species and their potential phytoplankton prey species over a large area at a single time. At the time of sampling, the plankton assemblage was diverse, and individual species had distinctive distributions related to the hydrography of the region, particularly to the location of the Irish Shelf Front, indicating possible niche differentiation. Although the sampling regime did not allow examination of species succession in the plankton community, our results illustrate the need to investigate the ecologies of different *Protoperidinium* species separately if we are to better understand plankton trophic dynamics. The distribution of *Protoperidinium* may be controlled by availability of prey, and *Protoperidinium* may exert important controls on the distributions and seasonality of their preferred prey species.

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REFERENCES

Archer, S. D., Leakey, R. J. G., Burkill, P. H. *et al.* (1996) Microbial dynamics in coastal waters of East Antarctica: herbivory by heterotrophic dinoflagellates. *Mar. Ecol. Prog. Ser.*, **139**, 1–3.

Balech, E. (1974) El genero *Protoperidinium* Bergh, 1881 (*Peridinium* Ehrenberg, 1831, Partim). *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigacion de las Ciencias Naturales*, **4**, 1–79.

Buskey, E. J. (1997) Behavioral components of feeding selectivity of the heterotrophic dinoflagellate *Protoperidinium pellucidum.*. *Mar. Ecol. Prog. Ser.*, **153**, 77–89.

Cusack, C., Silke, J., McDermott, G. *et al.* (2006) The Biological Oceanography of Harmful Algal Blooms (BOHAB) Programme: special emphasis on the dinoflagellate genus *Dinophysis*. *In 6th Irish Shellfish Safety Scientific Workshop*, pp. 55–63.

Dodge, J. D. (1982) *Marine Dinoflagellates of the British Isles*. Her Majesty's Stationery Office, London.

Dodge, J. D. (1994) Biogeography of marine armoured dinoflagellates and dinocysts in the NE Atlantic and North Sea. *Review of Paleobotany and Palynology*, **84**, 169–180.

Edwards, A., Jones, K. J., Graham, J. M. *et al.* (1996) Transient coastal upwelling and water circulation in Bantry Bay, a ria on the SW coast of Ireland. *Estuar. Coast. Shelf Sci.*, **42**, 213–230.

Fernand, L., Nolan, G. D., Raine, R. *et al.* (2006) The Irish coastal current: a seasonal jet-like circulation. *Cont. Shelf Res.*, **26**, 1775–1793.

Fileman, E. S. and Burkill, P. (2001) The herbivorous impact of microzooplankton during two short-term Lagrangian experiments off the NW coast of Galacia in summer 1998. *Prog. Oceanogr.*, **51**, 361–383.

Franks, P. J. S. and Anderson, D. M. (1992) Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. *Mar. Biol.*, **116**, 153–164.

Fritz, L. and Triemer, R. E. (1985) A rapid simple technique utilizing Calcofluor white M2R for the visualization of dinoflagellate thecal plates. *J. Phycol.*, **21**, 662–664.

Gaines, G. and Taylor, F. J. R. (1984) Extracellular digestion in marine dinoflagellates. *J. Plankton Res.*, **6**, 1057–1062.

Hasle, G. R. (1978) In Sournia, A. (ed.), *Phytoplankton Manual*. Monographs on Oceanographic Methodologies 6, UNESCO, Paris, pp. 191–196.

Huang, W. G., Cracknell, A. P., Vaughan, R. A. *et al*. (1991) A satellite and field view of the Irish Shelf front. *Cont. Shelf Res.*, **11**, 543–562.

Jacobson, D. M. and Anderson, D. M. (1986) Thecate heterotrophic dinoflagellates: feeding behavior and mechanisms. *J. Phycol.*, **22**, 249–258.

Jakobsen, H. H. and Hansen, P. J. (1997) Prey size selection, grazing and growth response of the small heterotrophic dinoflagellate *Gymnodinium* sp. and the ciliate *Balanion comatum*—a comparative study. *Mar. Ecol. Prog. Ser.*, **158**, 75–86.

James, K. J., Moroney, C., Roden, C. *et al*. (2003) Ubiquitous 'benign' alga emerges as the cause of shellfish contamination responsible for the human toxic syndrome, azaspiracid poisoning. *Toxicon*, **41**, 145–151.

Jeong, H. J. (1996) The predation impact by the heterotrophic dinoflagellate *Protoperidinium* cf. *divergens* on copepod eggs in the presence of co-occurring phytoplankton prey. *J. Oceanol. Soc. Korea*, **31**, 144–149.

Jeong, H. J. and Latz, M. I. (1994) Growth and grazing rates of the heterotrophic dinoflagellates *Protoperidinium* spp. on red tide dinoflagellates. *Mar. Ecol. Prog. Ser.*, **106**, 173–185.

Kjaeret, A. H., Naustvoll, L. J. and Paasche, E. (2000) Ecology of the heterotrophic dinoflagellate genus *Protoperidinium* in the inner Oslofjord (Norway). *Sarsia*, **85**, 5–6.

Lange, C. B., Hasle, G. R. and Syvertsen, E. E. (1992) Seasonal cycle of diatoms in the Skagerrak, North Atlatic, with emphasis on the period 1980-1990. *Sarsia*, **77**, 173–187.

Levinsen, H. and Nielsen, T. G. (2002) The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in Arctic and temperate coastal ecosystems: a cross-latitude comparison. *Limnol. Oceanogr.*, **47**, 427–439.

McMahon, T., Raine, R., Titov, O. *et al*. (1995) Some oceanographic features of northeastern Atlantic waters west of Ireland. *ICES J. Mar. Sci.*, **52**, 221–232.

McMahon, T., Raine, R. and Silke, J. (1998) Oceanographic control of harmful phytoplankton blooms around southwestern Ireland. In *VII International Conference on Harmful Algal Blooms*, pp. 128–129.

Menden-Deuer, S., Lessard, E. J., Satterberg, J. *et al*. (2005) Growth rates and starvation survival of three species of the pallium-feeding, thecate dinoflagellate genus *Protoperidinium*. *Aquat. Microb. Ecol.*, **41**, 145–152.

Moran, S., Silke, J., Salas, R. *et al*. (2005) Review of phytoplankton monitoring 2005. In Proceedings of the 6th Irish Shellfish Safety Scientific Workshop, pp. 4–10.

Naustvoll, L. J. (2000) Prey size spectra and food preferences in thecate heterotrophic dinoflagellates. *Phycologia*, **39**, 187–198.

Raine, R. (1996) Red tides and toxic phytoplankton in the southwest. *Aquacult. Ireland*, October/November, 26–27.

Raine, R. and 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.

Raine, R., O'Mahoney, J., McMahon, T. *et al*. (1990) Hydrography and phytoplankton of waters of South-west Ireland. *Estuar. Coast. Shelf Sci.*, **30**, 579–592.

Raine, R., Joyce, B., Richard, J. *et al*. (1993) The development of a bloom of the dinoflagellate *Gyrodinium aureolum* (Hulbert) on the south-west Irish coast. *ICES J. Mar. Sci.*, **50**, 461–469.

Raine, R., O'Boyle, S., O'Higgins, T. *et al*. (2001) A satellite and field portrait of a *Karenia mikimotoi* bloom off the south coast of Ireland, August 1998. *Hydrobiologia*, **465**, 187–193.

Raine, R., White, M. and Dodge, J. D. (2002) The summer distribution of net plankton dinoflagellates and their relation to water movements in the NE Atlantic Ocean, west of Ireland. *J. Plankton Res.*, **24**, 1131–1147.

Smetacek, V. (1981) The annual cycle of protozooplankton in the Kiel Bight. *Mar. Biol.*, **63**, 1–11.

Sukhanova, I. N., Flint, M. V., Witledge, T. E. *et al*. (2006) Mass development of the planktonic diatom *Proboscia alata* over the Bering Sea Shelf in the summer season. *Russ. Acad. Sci. Oceanol.*, **46**, 200–216.

Tillmann, U. and Hesse, K. J. (1998) On the quantitative importance of heterotrophic microplankton in the northern German Wadden Sea. *Estuaries*, **21**, 585–596.

Tiselius, P. and Kuylenstierna, M. (1996) Growth and decline of a diatom spring bloom: phytoplankton species composition, formation of marine snow and the role of heterotrophic dinoflagellates. *J. Plankton Res.*, **18**, 133–155.

Tomas, C. R. (ed.) (1997) *Identifying Marine Phytoplankton*. Academic Press, San Diego, CA.

Verity, P. G., Wassman, P., Frisher, M. E. *et al*. (2002) Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer. *J. Mar. Syst.*, **38**, 109–123.