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Large-scale impacts of bottom trawling on shelf primary productivity

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Abstract

Disturbance of the seabed resulting from bottom trawling affects ecosystem processes, such as the rate and magnitude of nutrient regeneration. The potential responses of the plankton community arising from such effects can be modelled, provided that reliable data on the effects on nutrient fluxes are available. In a north Cretan outer continental shelf and upper slope fishing ground (Heraklion Bay, Crete, Eastern Mediterranean) we applied a new field instrument which can simulate the passage of trawl groundropes across the sea floor and made direct seasonal measurements of the rate of dissolved and particulate nutrient releases resulting from seabed disturbance. These observational data were then integrated in a 3D ecosystem model. Results revealed that bottom trawling may trigger off considerable productivity pulses, in addition to pulses from the natural seasonal cycle.

Keywords: Bottom trawling; Ecosystem disturbance; Nutrient releases; Nutrient recycling; Resuspension; Primary production; Modelling

1. Introduction

Every year, the world fishing fleet comprising ca. 60,000 trawlers sweeps more than 15 million km^2 of seabed, mainly on the continental shelves (Watling and Norse, 1998). Commercial fishing has been identified as the primary anthropogenic disturbance not only in the intensively fished coastal areas of Europe and North America but, more recently, throughout the world (Jackson et al., 2001). The impact of the physical contact of bottom trawl fishing gear on the seabed produces a significant aftermath: it releases clouds of suspended sediment (Churchill, 1989; Palanques et al., 2001); it can both resuspend and bury biologically recyclable organic material (Mayer et al., 1991); it releases nutrients to the overlying water (Pilskaln et al., 1998; Durrieu de Madron et al., 2005); it is responsible for an increase in the mortality of benthic fauna (e.g., Hall, 1999).

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Though the potential of trawling to affect regional nutrient budgets has been noted (Pilskaln et al., 1998), yet direct measurements are rare (Durrieu de Madron et al., 2005; Dounas et al., 2005; Dounas, 2006). Resuspension of bottom sediments in coastal waters stimulates water column microbial production (Wainright, 1987; Ritzrau and Graf, 1992; Gotner et al., 2000), causing a substantial increase in total system organic matter mineralisation (Wainright and Hopkinson, 1997; Dale and Prego, 2002) which may persist for much longer (from days to weeks) than the resuspension event itself (Wainright, 1990). Suspended particulate matter by natural hydrodynamic forcing is advected very close to the seabed rather than whisked high into the water column in both shallow (Leipe et al., 2000) and deep sea environments (Thomsen et al., 2002). This transport in proximity to the sediment–water interface has important implications for the distribution of organic matter as food for benthic suspension feeders (Beaulieu, 2002, 2003). In contrast, sediment mechanically resuspended by trawling extends, in significant concentrations, to more than 10 m above the bottom (Churchill, 1989 and references therein; Pilskaln et al., 1998). This process may further prolong the exposure of sedimentary organic matter to oxic conditions, accelerate mineralisation and decrease denitrification rates, thereby making more nitrogen available to phytoplankton (Wainright and Hopkinson, 1997). The effects of bottom trawling-induced disturbance on large-scale ecosystem processes, such as nutrient regeneration and primary productivity, are still difficult to predict for open coastal and outer shelf ecosystems where most trawling activity is concentrated (National Research Council, 2002).

We performed seasonal observations of the sediment resuspension by using a benthic sledge adapted to simulate the passage across the sea floor of a trawl groundrope typical of the kind (commonly) used in the Cretan fisheries (Dounas, 2006). Previous experimental results indicated that almost all the biologically active compounds of the sediment are resuspended by a single passage of the trawl-simulating gear implying that the upper, extremely thin, layer of shelf non-permeable sediments (<1 mm) contains a considerable reservoir of dissolved and particulate nutrients in much higher concentrations than in the immediately underlying surface layers (Dounas et al., 2005). These results are consistent with new findings which also suggest that in shelf muddy bottoms the particulate matter load injected by a trawling rig into the water column comes from the resuspension of less than 1 mm thickness of the surface sediment (Durrieu de Madron et al., 2005). Thus, the new sampling apparatus enables direct measurements of the amount of sediment and nutrients raised into suspension per unit length of trawl track or seabed surface area. These observational data were integrated in a 3D ecological model in order to investigate potential large-scale effects of bottom trawling on shelf primary productivity which was the major aim of this study.

2. Methods

2.1. Study area

All field experiments were conducted in the outer continental shelf and upper slope of Heraklion Bay (Cretan Sea) at 100, 200 and 300 m depths (Fig. 1) on four occasions: April, June, October 2000 and February 2001. The sea floor sediment is predominantly mud, with low organic carbon concentrations and positive redox potential values (Tselepides et al., 2000a). The area is characterised as oligotrophic with mean annual gross primary productivity of 80 and 59 g carbon $m^{-2} year^{-1}$ on the shelf and slope, respectively (Psarra et al., 2000).

The circulation in the broader study area (central Cretan Sea) is influenced by a mesoscale dipole consisting of two gyres (Fig. 1), an anticyclonic eddy in the West and a cyclonic eddy in the East (Theocharis et al., 1999; Hamad et al., 2006). The experimental sampling stations were located at the basis of the boundary zone between these aforementioned eddies, an area dominated by a very stable southward current that turns gradually to a SE–ESE direction when it reaches the upper slope and the continental shelf of Heraklion Bay (Georgopoulos et al., 2000). According to Tselepides et al. (2000b), this particular circulation in the central Cretan Sea acts as a pump, transporting water masses southward and upwelling them up onto the euphotic zone of the Cretan continental shelf.

Before sampling, the study area was surveyed by underwater towed-video operations. Heavy commercial trawling activity was indicated especially at the 100 m depth sampling station, as evidenced by numerous heavy plough furrows (door impacts), lightly scraped sediment surfaces (wire impacts) and completely flattened and scraped surfaces (groundrope and net impacts). These impacts have also been recorded by Smith et al. (2003) from the

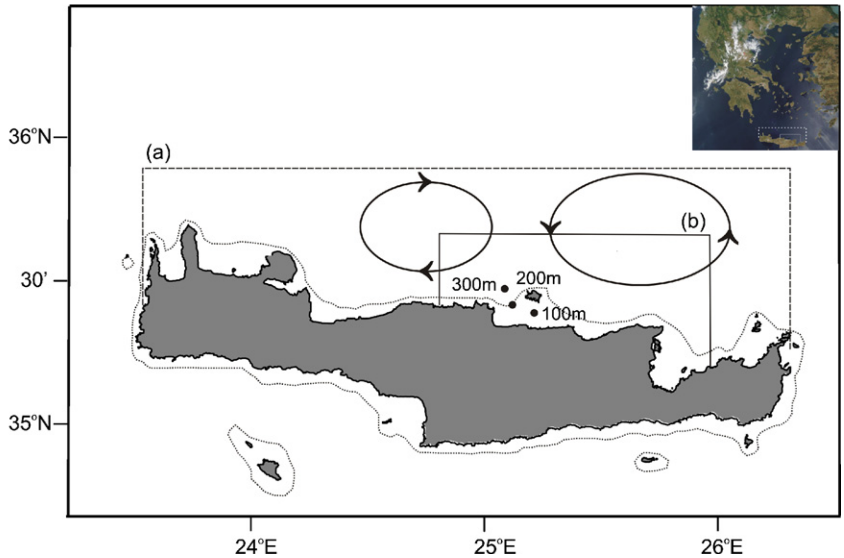

Fig. 1. Map of the South Aegean Sea area with (a) coarse and (b) fine resolution model domains and the position of the main circulation features in the study area according to Theocharis et al. (1999). Depth contour represents the continental shelf limit (200 m).

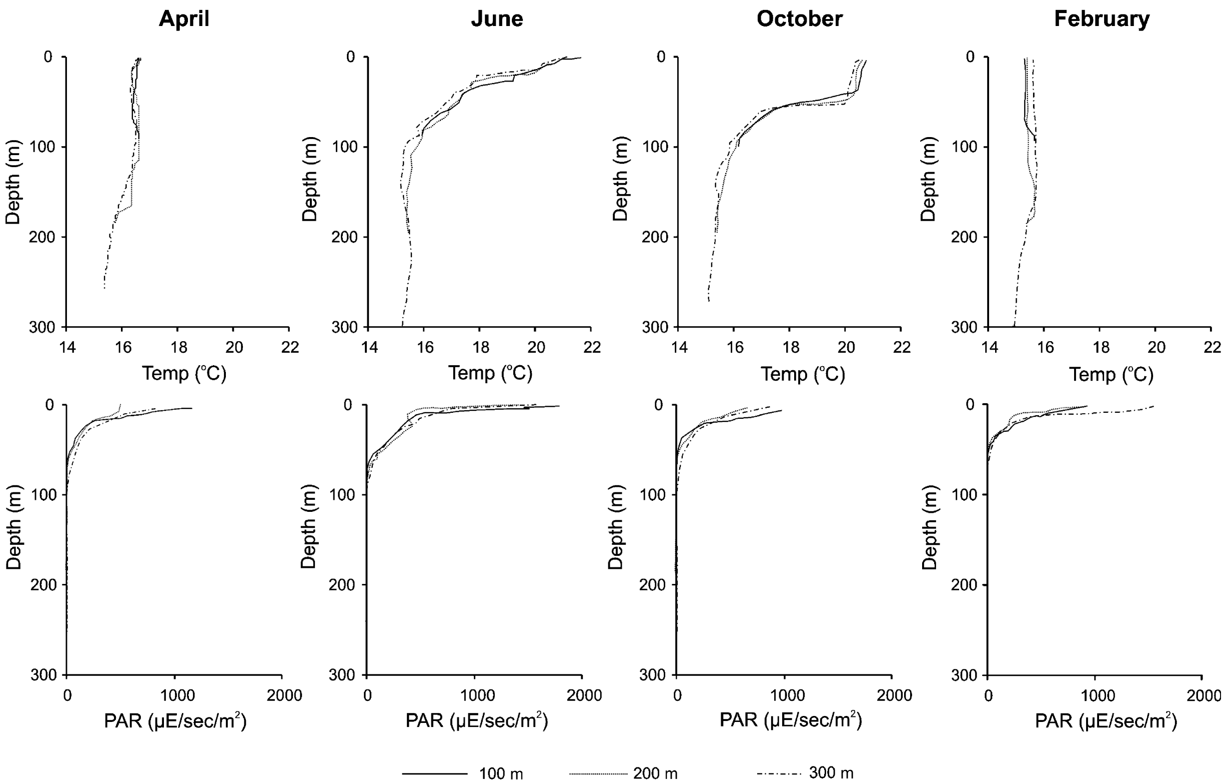

Fig. 2. Vertical profiles of temperature and photosynthetic active radiation (PAR) at the three sampling stations (100, 200 and 300 m).

same area. The physical parameters of the water column were recorded with a Sea-Bird Electronics (SBE-25) CTD system. Throughout the experimental period the euphotic zone extended down to 40–60 m at the shelf stations and down to 50–80 m at the slope station, while during summer and autumn sampling periods there was a prominent thermocline between 60 and 80 m depth (Fig. 2).

2.2. Field experiments

The experimental sampling gear used in this study was a towed trawl simulator sledge (TTSS) described by Dounas (2006). This sampling instrument is designed to simulate the disturbance of sediments by trawl groundropes, and at the same time it allows direct sampling of water to be carried out in the plume of the disturbed sediment behind the groundrope. It is constructed around the frame of an existing towed benthic sledge (Shand and Priestley, 1999) modified to incorporate one or more lengths of otter trawl groundrope between the forward parts of the runners of the sledge, in contact with the sediment surface. Horizontal water samplers are mounted internally at the front and sides of the sledge and arranged in rows above the seabed surface. One electromagnet is mounted on each bottle and holds both end closures in the open position against pre-tensioned springs. On command from the surface, the electromagnets are turned off, closing the water samplers simultaneously. A colour video camera located in the upper part of the sledge records the performance of the whole underwater apparatus.

Three TTSS tows were performed in each station. In each tow, we collected water samples from the 6×21 Hydrobios water bottles mounted horizontally in pairs at 2.5, 17.5 and 30 cm above the seabed, located 1 m behind the groundrope, in front of any disturbance caused by the framework and runners of the sledge, and in the middle of the sediment cloud caused by the groundrope. Continuous monitoring by the video camera attached to the sledge showed that resuspension of sediment ahead of the sampling bottles was caused solely by the groundrope. R.V. *Philia* towed the sledge at normal trawling speed (ca. 2.2 knots). Three additional TTSS tows were performed without the groundrope and collected water samples used as reference. These data collections were interspersed between deployments of TTSS with groundropes in order to take into account the variability of control conditions. Finally, 51 Niskin bottles were used to sample the water column at standard depths (1, 10, 20, 50, 75, 99, 150, 199, 250, 299 m) wherever possible at each station.

For the determination of chlorophyll *a* (chla), phaeopigments, particulate organic carbon (POC), particulate organic nitrogen (PON), as well as total solid concentrations, all samples were filtered through Whatman GF/F glass fibre filters. Water sub-samples (200 ml) were collected from the filtrate for nutrient analysis (PO_4, SiO_2, NH_4, NO_2, NO_3), frozen immediately, and finally stored at $-20\,^{\circ}C$ until analysis upon return to the laboratory. Chlorophyll *a* and chloroplastic pigment equivalent (CPE) were determined according to the fluorometric method of Yentsch and Menzel (1963), using a Turner 112 fluorometer. The POC and PON concentrations were analysed using a Perkin-Elmer CHN 2400 analyzer according to Hedges and Stern (1984). Nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), phosphate (PO_4), and silicate (SiO_2) concentrations were determined using a Beckmann DU65 spectrophotometer according to the methodology of Strickland and Parsons (1972).

Inventories of the experimentally resuspended material were calculated from sets of three by six water samples, corrected by subtracting measurements made under "reference" conditions (water samples collected using the sledge omitting the groundrope in the same areas) and expressed as quantities resuspended per area of disturbed sediment. Finally, application of the towing speed allowed calculation of the resuspension rate of materials per unit of trawling time.

2.3. Ecosystem model simulations

In recent years, ecosystem models have increasingly been considered as management tools. With respect to potential fisheries impacts, dynamic ecosystem models can provide significant insights into the governing processes and can also predict a number of scenarios that would otherwise be both expensive and time consuming to apply in the field. Thus, in order to move towards an improved understanding of the underlying dynamics and to evaluate the effects of trawl-induced disturbance on large-scale ecosystem processes, we integrated the measured *in situ* data for each sampling period in a tuned and validated 3D ecosystem model for the Cretan Sea area.

The ecosystem model consists of two highly portable, on-line coupled sub-models: the 3D Princeton Ocean Model (POM) (Blumberg and Mellor, 1987), and the European Regional Seas Ecosystem Model (ERSEM) (Baretta et al., 1995). POM describes the hydrodynamics of the area and provides the background physical information to the ecological model. It is a primitive equation, time-dependent, σ-coordinate, free surface, and split-mode time step model, calculating the equations of velocity ($Ui = (U, V, W)$), temperature (T), and salinity (S). For the eddy diffusivity parameters the second moment turbulence closure sub-model of Mellor and Yamada (1982) is used, while the horizontal parameters F_U, F_V, F_T, and F_S are calculated through the Smagorinsky (1963) formulation. Finally, the density is calculated from the UNESCO equation of state adapted by Mellor (1991). The model domain was Heraklion Bay which formed a horizontal grid of 32×12 boxes with dimensions 2.783×2.253 km. In the vertical there were 25 equally spaced boxes, following the model bathymetry constructed from the US Navy Digital Bathymetric Data Base—DBDB5—and from *in situ* measurements from the R/V *Philia*. The initial fields as well as monthly profiles of temperature and salinity were provided by the Mediterranean Forecasting System Towards Environmental Predictions Project (MFSTEP). For the atmospheric forcing monthly fields of wind stress components, net heat flux, net short-wave radiation and evaporative heat flux were used from the 6-h 1979–1993 ECMWF re-analysis for Heraklion Bay. Cloud cover data necessary for heat flux computations were taken from COADS 1979–1993 monthly dataset, while monthly SST fields for the same period came from Reynolds. To confront the problems at the open boundaries the model was one-way nested with the coarser Cretan Sea model covering the area between 23.575–26.3°E and 35.075–36°N with a grid resolution of 1.5 min (Triantafyllou et al., 2003a, b).

The ecological model is a comprehensive ecosystem model, which dynamically simulates the large-scale cycling of organic carbon, oxygen and macronutrients N, P and Si in both pelagic and benthic components. This model has been evaluated as the most suitable for generating quantitative, testable predictions concerning the response of the ecosystem to fishing effects and especially the knock-on effects of resuspension on primary production and nutrient cycling (Robinson and Frid, 2003). ERSEM uses a functional approach, grouping organisms according to their role in the system and not according to species. The whole model structure is built around the dynamics of carbon cycling, while nutrients although coupled on it have dynamically varying ratios, depending on the specific internal ratio within each functional group and the external availability. The food web is a compromise between the need for a realistic representation of the biogeochemical processes and at the same time for a degree of simplification and aggregation.

The coupling of the two sub-models is through the following equation which is solved for the concentration of carbon for each functional group of the pelagic system:

$$\frac{\vartheta C}{\vartheta t} = -U\frac{\partial C}{\partial x} - V\frac{\partial C}{\partial y} - W\frac{\partial C}{\partial z} + \frac{\partial}{\partial x}\left(A_H\frac{\partial C}{\partial x}\right) + \frac{\partial}{\partial y}\left(A_H\frac{\partial C}{\partial y}\right) + \frac{\partial}{\partial z}\left(K_H\frac{\partial C}{\partial z}\right) + \sum BF$$

where U, V, W are the velocity field components, A_H the horizontal viscosity coefficient, and K_H the vertical eddy mixing coefficient, provided by POM. The last term accounts for the total biochemical flux, calculated by ERSEM, for each pelagic group. The equation is approximated by a finite-difference scheme and is solved in two time steps (Mellor, 1991): an explicit conservative scheme for the advection (Lin et al., 1994), and an implicit one for the vertical diffusion (Richtmyer and Morton, 1994). A detailed description of the ecosystem model used in this study together with its application, calibration and validation for the Cretan Sea has been presented elsewhere (Petihakis et al., 2002; Triantafyllou et al., 2003a–c; Hoteit et al., 2004).

As mentioned above, in an attempt to analyse and evaluate the effect of trawling on large-scale ecosystem processes, such as nutrient regeneration and primary productivity, a series of experimental runs was performed. The principal aim was to force the ecosystem model with the dissolved and particulate nutrient releases as measured seasonally in the field at the three sampling stations (Fig. 1). The main hypothesis was that a bottom trawler works approximately 8 h in 1 day covering an area of about 1.3×10^6 m^2 (2.2 knots towing speed, 40 m sweep length). Thus, we introduced inorganic nutrients and particulate organic matter injections in the model in the first 80 integration steps, i.e., covering the period of the first 8 h with a time step of 360 s and afterwards the model ran for 2 months. To adjust the calculated trawled area into the model grid the injected material was uniformly diluted to a volume described by the horizontal dimensions ($dx \times dy$) of each grid box and to a height of 10 m from the bottom which coincides with the height of suspended sediment plumes in the wake of bottom trawling reported in the literature (Churchill, 1989).

In order to evaluate trawling effects prior to the experimental runs, a reference run was performed where the system was simulated under the same conditions of forcing but without any trawling. Thus, the simulated primary production derived from each experiment could be compared on a day-to-day basis, integrated both horizontally and vertically, with the reference system simulation, in order to obtain estimates of the net increases in primary production (expressed as carbon fixation) for a period of 2 months.

3. Results

The water column reference concentrations of the different dissolved and particulate elements measured, by using either TTSS (without the groundrope) close to the seabed or Niskin bottles for the upper level of the water column, are given in Table 1. It should be noted that total inorganic nitrogen concentration within the benthic boundary layer (0–0.5 m above seabed) at all sampling periods and depths was always two to three times higher than the upper water layers. Exceptionally, during the winter sampling period inorganic nitrogen compounds were evenly distributed throughout the water column most probably due to intense vertical mixing. Inorganic phosphate and silicate concentrations were also more or less evenly distributed throughout the water column during all sampling periods. Average water column POC and nitrogen concentrations were one order of magnitude higher in April and October than in June and February. Respectively, particulate organic matter concentrations close to the seabed were generally characterised by much higher variation than the upper water layers. During all periods except for February particulate organic matter C/N ratio values were relatively low within the benthic boundary layer (7.8–12.5) while in the upper water column average C/N ratio values varied from 12.1 to 24.6. In February C/N ratio values remained low throughout the water column (7.8–8.9).

Table 2 shows the inventories of the experimentally resuspended particulate and inorganic nutrients calculated from six sets of water samples collected at each sampling station by using the TTSS (Dounas, 2006). These measurements were introduced into the model in 80 equal injections each with a time step of 360 s covering an 8-h period of continuous trawling at each station.

Model simulation of bottom trawling revealed a considerable increase in the depth integrated carbon fixation at both 100 and 200 m stations in all seasons, with the sole exception of the autumn simulation run at 200 m (Fig. 3). Since the modelled system is mainly nutrient limited the influx of nutrients in the model and in particular in the euphotic zone triggers phytoplankton growth with subsequent carbon fixation. At the deeper station (300 m) there was no difference between the reference run and the run with additional inputs due to seabed disturbance. This was to be expected because of the greater depth of the water column and the consequent lower nutrient releases compared to the two shallower stations. The total quantity of additional carbon fixed over the Cretan Sea, as estimated by the model, was 9.9 tonnes in autumn at 100 m depth but only 100 kg at 200 m in the same season. At the shallow station, there was a time lag of 1 day in the phytoplankton response to increased nutrients, with net primary production reaching maximum values during the course of the first week. Exceptionally, during autumn, two peaks were produced (7 and 15 days) with the second peak being considerably higher. At the 200 m experimental site, the time lag predicted was approximately 5–6 days and maximum values were reached within the first 16 days.

The spatial distribution of the net primary production increase, integrated both in depth and time, exhibited a marked seasonal variation (Fig. 4). In the case of the 100 m depth run, all the impacted areas were within the shallow part of the shelf extending eastwards up to as far as 60 km, covering a maximum total area of 344 km^2 in autumn. Inputs simulated at the intermediate site (200 m), resulted in smaller increases in net primary production. The underlying mechanism is the advection of nutrients, which have been remineralised in the water column, southward and towards the proximal coastal zone away from the sites of disturbance, and the subsequent increase in productivity when these nutrients enter the euphotic zone. An interesting result was the extended signal in spring which covered a large part of the simulation field, forming an almost continuous coastal belt and covering a total area of 188 km^2. Seasonally averaged quantities of additional carbon fixed per m^2 of seabed disturbance were 4.6 and 0.9 g C at the 100 and 200 m stations, respectively.

The average fishing time in the Cretan fishery is 163.5 days $year^{-1}$ and 12.6 h day^{-1} (Hellenic Centre

Table 1
Mean seasonal values of water column reference inorganic and particulate nutrient concentrations measured at different depths and at different levels above seabed

Sampling month	Total inorganic nitrogen ($\mu M\,l^{-1}$)		Total inorganic phosphate ($\mu M\,l^{-1}$)		Total inorganic silicate ($\mu M\,l^{-1}$)		Total particulate carbon ($\mu g\,l^{-1}$)		Total particulate nitrogen ($\mu g\,l^{-1}$)	
	0–0.5	1–99	0–0.5	1–99	0–0.5	1–99	0–0.5	1–99	0–0.5	1–99
Depth 100 *m* (*distance above seabed* (*m*))										
April	1.3±0.3	0.6±0.3	0.04±0.02	0.05±0.02	5.9±2.6	5.6±0.9	78.4±8.7	405.00±75.62	10.6±1.9	30.9±9.5
June	2.0±0.3	0.4±0.2	0.02±0.01	0.05±0.03	1.8±0.3	1.4±0.2	153.2±74.3	59.16±10.29	23.4±3.7	5.7±1.2
October	6.3±0.9	4.7±0.8	0.05±0.01	0.09±0.06	5.9±1.3	5.6±0.6	275.8±254.8	429.00±89.85	41.3±20.0	27.1±4.3
February	6.0±1.4	6.2±2.1	0.05±0.01	0.03±0.02	3.7±0.8	3.7±1.7	285.3±114.4	47.90±8.12	39.0±18.23	6.9±1.2
	0–0.5	1–199	0–0.5	1–199	0–0.5	1–199	0–0.5	1–199	0–0.5	1–199
Depth 200 *m* (*distance above seabed* (*m*))										
April	2.3±0.5	0.8±0.4	0.05±0.01	0.03±0.02	5.6±2.8	4.0±3.5	138.1±46.4	451.00±79.11	15.0±1.9	25.2±5.1
June	3.0±0.4	1.6±0.2	0.02±0.01	0.07±0.05	2.1±0.4	1.6±0.9	115.3±52.4	48.51±21.69	13.2±9.0	2.3±2.4
October	10.8±0.9	5.1±1.0	0.07±0.01	0.10±0.06	9.6±2.9	4.7±0.4	113.5±47.3	328.33±70.45	15.3±6.2	18.6±4.4
February	7.9±2.6	7.2±2.7	0.10±0.05	0.07±0.02	3.6±1.8	2.4±1.9	196.9±107.4	45.51±15.36	29.6±21.1	6.3±1.9
	0–0.5	1–299	0–0.5	1–299	0–0.5	1–299	0–0.5	1–299	0–0.5	1–299
Depth 300 *m* (*distance above seabed* (*m*))										
April	3.1±0.5	1.3±1.8	0.14±0.02	0.03±0.02	4.2±1.0	1.7±1.0	412.5±51.6	435.0±139.4	53.7±6.8	28.1±12.4
June	3.0±0.9	0.4±0.1	0.18±0.31	0.19±0.06	1.9±0.2	1.9±1.5	111.8±93.9	41.0±21.7	27.4±12.9	1.9±1.8
October	12.8±1.3	5.6±1.3	0.18±0.01	0.16±0.20	7.5±3.8	5.7±0.5	114.2±30.1	300.2±105.7	21.0±6.2	17.3±10.5
February	7.8±0.4	7.6±3.2	0.12±0.06	0.15±0.04	3.1±0.5	4.2±2.5	278.4±126.1	38.7±11.9	37.4±18.2	5.1±1.8

Table 2
Net nutrient releases[a] to the overlying water by experimental bottom trawling

Sampling period	μM N m^{-2}	μM P m^{-2}	μM Si m^{-2}	POC g m^{-2}	PON g m^{-2}
	Depth 100 m				
April	727.02±327.65	44.14±12.98	666.33±470.75	3.81±1.28	0.40±0.14
June	652.78±124.81	56.88±10.32	752.05±396.90	2.36±1.37	0.34±0.19
October	752.76±186.09	78.88±21.54	663.20±422.68	4.06±0.80	0.61±0.17
February	630.25±114.46	51.75±8.67	360.36±166.36	1.98±0.72	0.28±0.15
	Depth 200 m				
April	402.16±225.70	30.11±17.17	749.65±122.69	4.01±1.03	0.33±0.08
June	270.81±159.84	34.13±8.47	536.60±209.39	1.21±0.29	0.17±0.04
October	635.44±380.28	30.13±11.24	407.25±171.10	1.18±0.46	0.12±0.02
February	295.88±124.46	25.31±13.17	211.88±136.43	1.02±0.95	0.10±0.02
	Depth 300 m				
April	128.84±160.81	22.55±14.45	704.55±172.09	0.85±0.38	0.06±0.03
June	232.56±150.68	19.25±16.69	525.83±219.76	0.45±0.26	0.05±0.03
October	293.89±126.16	23.06±3.54	354.00±298.70	0.90±0.11	0.07±0.02
February	84.75±40.81	17.81±4.76	174.38±69.24	0.58±0.31	0.04±0.02

[a]Mean±S.D. from three independent tows of the towed trawling simulating sledge (TTSS).

for Marine Research, unpublished data). A trawling speed of 2.2 knots (1 m s^{-1}) and a trawl sweep of 40 m results in a total swept shelf area of $330\times10^{6}\,m^{2}\,year^{-1}$, i.e. a surface approximately equal to the continental shelf of Heraklion Bay (376 km^2). The seasonally averaged quantity of additional carbon fixed due to trawling disturbance estimated from the intensely fished 100 m depth station, suggests that a single vessel might be responsible for the assimilation of 1.54×10^{12} mg C $year^{-1}$. This amount is equivalent to about 5% of the total annual primary production over the entire shelf area. These data suggest that over the 9-month fishing period the nutrient ''by-product'' produced by the local fishing fleet (two to three trawlers) can support up to 15% of the total annual primary production in the Heraklion Bay fishing grounds.

4. Discussion

Heraklion Bay, centrally located in the north coast of Crete, is considered as one of the best studied regions in the Eastern Mediterranean (Tselepides and Polychronaki, 2000). The area is characterised by intrusions of Transition Mediterranean Water (TMW) rich in nutrients, which along with the mesoscale dipole circulation and the seasonal stratification of the water column, are the main factors controlling this marine ecosystem (Georgopoulos et al., 2000). According to Tselepides et al. (2000b), the organic matter produced offshore in the surface waters during the late-winter/early-spring mixing periods eventually sinks to depths from 200 to 400 m where it becomes trapped as a result of the progressive onset of stratification. Under the influence of the mesoscale dipole and the strong southward tendency of the currents, waters rich in POM are transported towards the shelf thus fertilising the coastal proximal zone with nutrients. *In situ* experimental measurements and model results from this study are in full accordance with the afore-mentioned nutrient transport and upwelling mechanism. Thus, the particulate and inorganic nutrients injected into the water column due to bottom trawling sediment disturbance are also advected southward, resulting in considerable increases of primary productivity when they enter the coastal euphotic zone as revealed by model experimental results.

With the exception of the present study carried out in Heraklion Bay, the only other direct experimental measurements of dissolved and particulate matter resuspended by bottom trawling are reported from the continental shelf of the Gulf of Lion, NW Mediterranean (Durrieu de Madron et al., 2005).

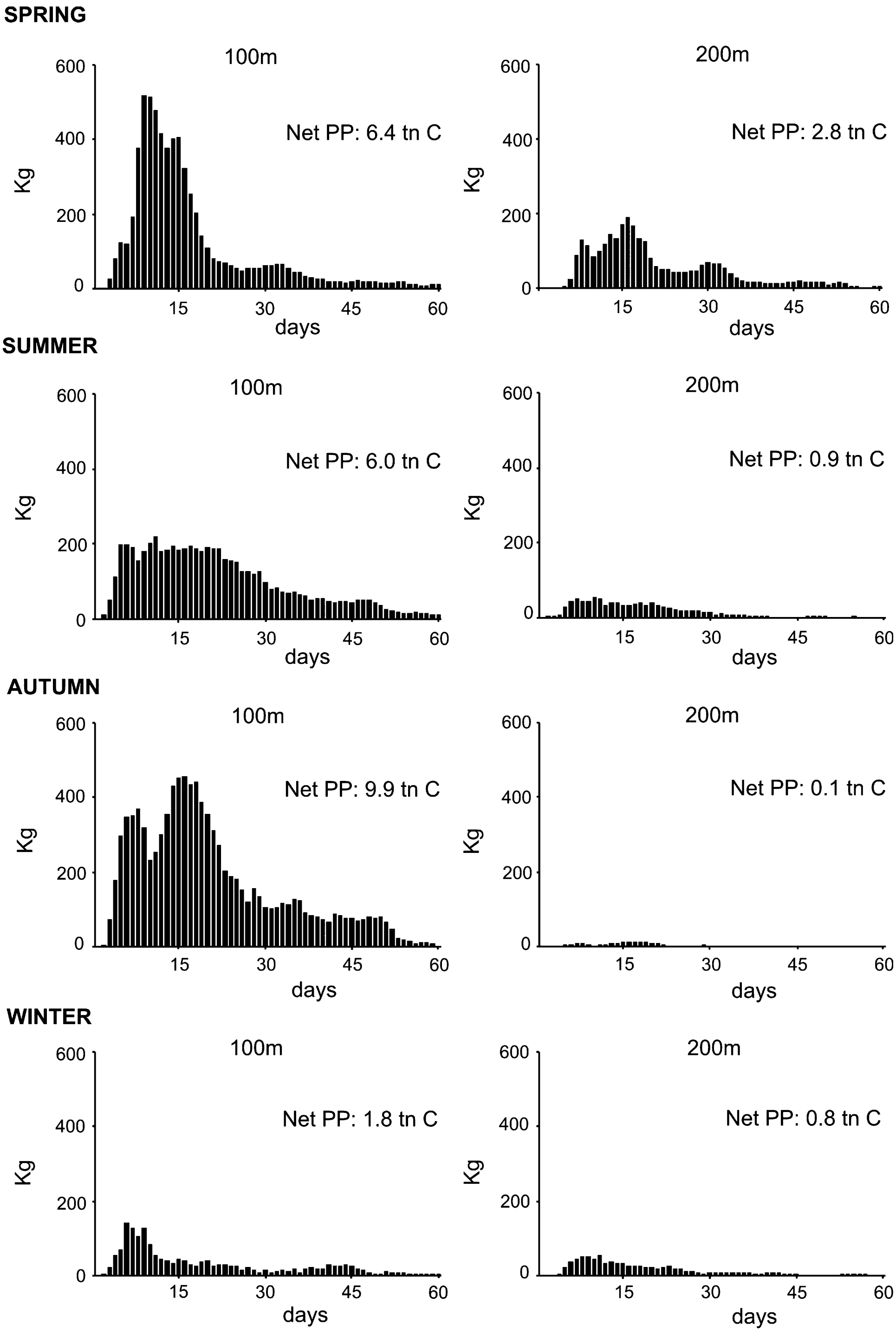

Fig. 3. Daily spatially and depth integrated increases of net primary production due to 8 h trawling simulation experiments at 100 and 200 m stations. The total quantity of additional carbon fixed in a period of 60 days is also given.

A comparison of the resuspension by bottom trawling fluxes of inorganic and particulate nutrients estimated for the two areas is given in Table 3. Trawling-induced nutrient fluxes are of the same order of magnitude with slightly higher values in most of the nutrients measured in the Gulf of Lion,

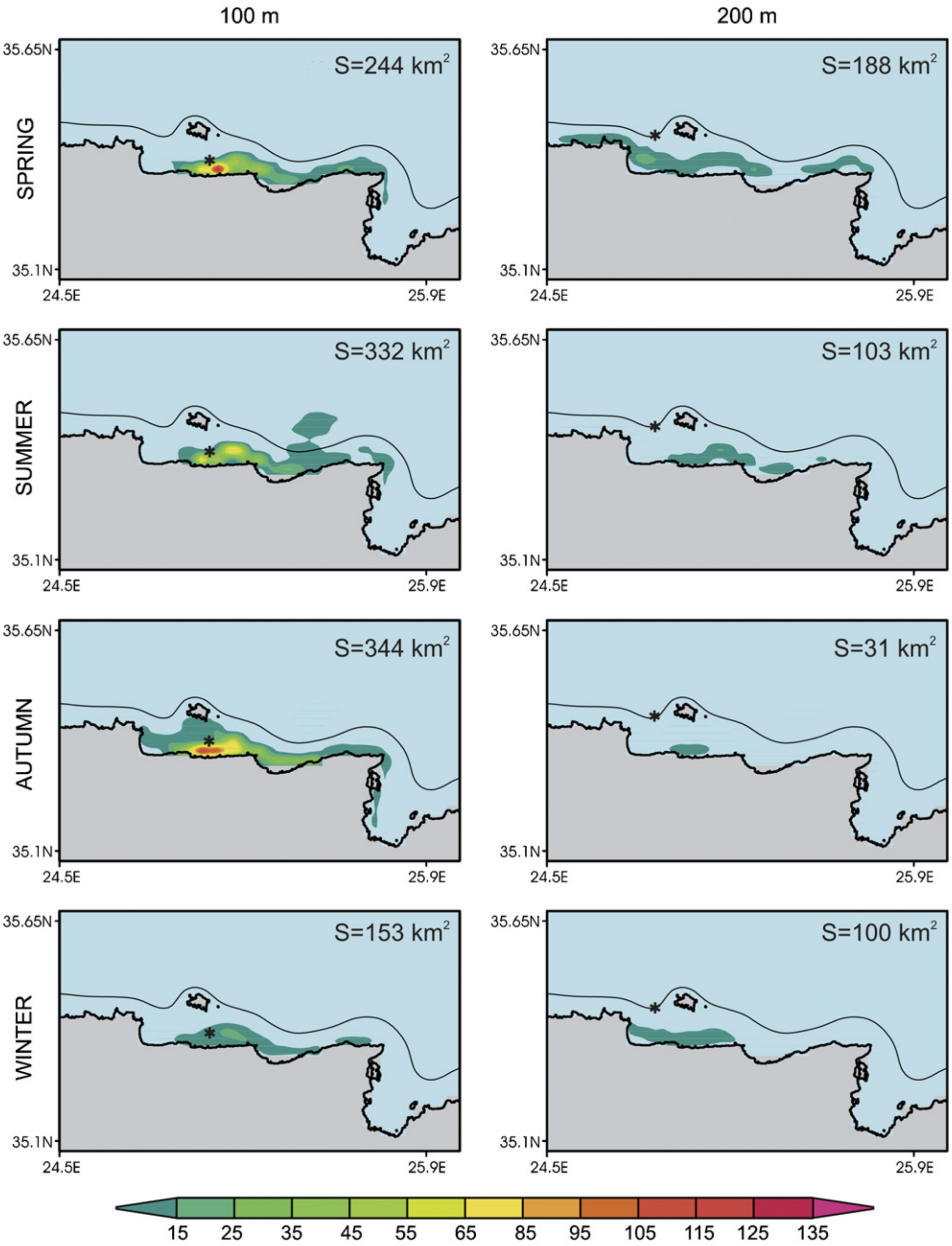

Fig. 4. Seasonal depth integrated spatial distribution of additional carbon fixed due to 8 h trawling simulations in 100 and 200 m depth accumulated over a period of 60 days. Total surface impacted (*S*) is given in km^2. Net primary production units are in $mg\,C\,m^{-2}\,60\,days^{-1}$. Station positions are indicated with an asterisk.

most probably due to the higher annual gross primary productivity recorded in this area, i.e. $80\,g\,C\,m^{-2}\,year^{-1}$ in Heraklion Bay (Psarra et al., 2000) and 86–142 $g\,C\,m^{-2}\,year^{-1}$ in the Gulf of Lion (Lefevre et al., 1997).

Despite the fact that bottom trawling still remains, even today, the predominant offshore human activity research on habitat disturbance by trawling has been limited to experimental disturbance of animal communities rather than on large-scale ecosystem processes such as nutrient regeneration and primary productivity (National Research Council, 2002). According to relatively recent conservative estimates, a very large area equivalent to 53–76% of the world's continental shelf ($27\times10^6\,km^2$) is swept annually by bottom trawling (Watling and Norse,

Table 3
Comparison of bottom trawling resuspension fluxes of inorganic and particulate nutrients measured in the Gulf of Lion and the Cretan shelf

Fluxes	Gulf of Lion, depth: 90 m; >82% silt and clay (Durrieu de Madron et al., 2005)	Gulf of Heraklion, depth: 100 m; >80% silt and clay (this study)
N ($\mu M\,m^{-2}$)	1870	653
P ($\mu M\,m^{-2}$)	90	57
Si ($\mu M\,m^{-2}$)	300	752
POC ($g\,m^{-2}$)	3.2	2.4
PON ($g\,m^{-2}$)	0.6	0.3
Suspended sediment ($g\,m^{-2}$)	540	290

1998). By applying the seasonally averaged fluxes of dissolved and PON per m^2 of seabed disturbance measured for the oligotrophic Cretan shelf (100 m station, Table 1), we can estimate that large quantities of nutrients, e.g., 0.14–0.20 Tg of dissolved N or 5.9–8.4 Tg of particulate organic N, may be injected annually into the water column as a result of the world trawling fleet activities. According to the model predictions from the trawling disturbance experiments performed in Heraklion Bay, the additional nutrients upwelled in the proximal coastal area could be responsible for an increase of up to 15% of the net annual primary production recorded for the entire continental shelf area of the Bay. Nevertheless, it is not feasible at this early stage to make valid comparisons with other heavily exploited and more productive fishing grounds, such as the North Sea or Georges Bank, as the impact of the resuspended by trawling nutrients on the ecosystem, as shown in this study, depends heavily upon the prevailing local hydrographic and environmental conditions.

During the latter part of the 20th century, wild capture fisheries in many parts of the world oceans show a steady change to lower mean trophic levels and a reduction in the ratio of piscivorous to zooplanktivorous fish (PS/ZP) (Pauly et al., 1998). The possible cause(s) of these changes continue to be debated, and include the removal of large predators (fishing down the marine food web concept), increased pelagic primary production, market changes or technological developments, and long-term environmental or ecological changes (Caddy and Garibaldi, 2000). All these changes have been accompanied by increases in the fishing capacity of the world fleet (Pauly et al., 2002). Our experiments indicated that disturbance of the seabed by bottom trawl gear (affecting the coupling between the processes of benthic recycling and primary production) can increase the recycling rate of nutrients from the benthic to pelagic environments. This could support "bottom-up" mechanisms for increasing the amount of food available to planktivorous fish in nutrient-limited systems. The ratio PS/ZP could thereby be decreased without the need to postulate acute negative impacts on the stocks of demersal benthivorous and piscivorous species caused by reduced oxygen levels in bottom waters as a consequence of increased land run-off and eutrophication of the proximal coastal zone (de Leiva Moreno et al., 2000). Moreover, trawling-induced changes on the biogeochemical cycling of carbon and nutrient elements may act synergistically with other natural and human disturbances (Jackson et al., 2001; Rabouille et al., 2001), favouring the occurrence of undesirable algal blooms (Pilskaln et al., 1998).

5. Conclusions

Sediment disturbance by bottom trawling may transfer considerable amounts of dissolved and particulate nutrients from benthic to pelagic systems. Subsequently, remineralised in the water column nutrients may be transported back to the euphotic zone to support new production. In Heraklion Bay, it is the local circulation regime which is responsible for the southward advection of resuspended nutrients away from the sites of bottom trawling disturbance and up to their final upwelling into the euphotic zone. Though these pulses of productivity could have significant effects for eutrophication of the continental shelf, they are rarely, if ever, taken into account in fisheries and marine ecosystem management. Future research on the effects of bottom trawling impact should include the study of the rates and magnitude of sediment resuspension, nutrient recycling, and responses of the plankton community in relation to trawl-induced disturbance.

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