American Fisheries Society Symposium 41:529–537, 2005

Preliminary Results on the Effect of Otter Trawling on Hyperbenthic Communities in Heraklion Bay, Cretan Sea, Eastern Mediterranean

PANAYOTA T. KOULOURI[1] AND COSTAS G. DOUNAS[2]
Institute of Marine Biology of Crete, Post Office Box 2214, GR-71003, Heraklion, Crete, Greece

ANASTASIOS ELEFTHERIOU[3]
Department of Biology, University of Crete, Post Office Box 2208, GR- 71409, Vassilika Vouton, Heraklion, Crete, Greece

Abstract. Although the benthopelagic fish species are a focus of commercial exploitation, relatively little attention has been paid to the small-sized invertebrates (0.5–20 mm) living on or very close to the seabed, thus inhabiting the same biotope, known also as hyperbenthos. Recently, interest in this faunal group has increased, as many demersal fish and epibenthic crustaceans have been found to feed on hyperbenthic animals for at least part of their lives. Otter trawls, the most common gear used for demersal fishing, result in significant disturbance of the sediment–water interface. Animals that are disturbed by the passage of a trawl may become more available to predators and scavengers. We have been unable to find any reports of studies of the impacts of towed fishing gears, including otter trawls, on hyperbenthos. We studied these effects on the Mediterranean continental shelf in Heraklion Bay (Cretan Sea) using a novel apparatus to simulate the contact of otter trawl groundrope with the seabed. A modified three-level hyperbenthic sledge was used for collecting disturbed (groundrope present) and undisturbed (without groundrope) macrofaunal samples at a towing speed typical of the local commercial vessels. Observations were made before and during the trawling season in an area being actively fished. The preliminary results reported here indicate that trawling causes significant changes in the structure of hyperbenthic communities.

Introduction

Otter trawls, the most common gear used for demersal fishing, have been reported to disturb the seabed sediment to depths of up to a few centimeters below the sediment–water interface (Lindeboom and de Groot 1998). Many studies have shown that benthic infauna and epifauna can be exposed, damaged, or killed by the passage of a trawl and that this may lead to increased opportunistic feeding by invertebrate and fish predators (Jennings and Kaiser 1998; Hall 1999; Kaiser and de Groot 2000). However, no reports on the effects of demersal fishing gears, particularly otter trawls, on hyperbenthic fauna were found.

The term "hyperbenthos" is defined as the 0.5–20-mm bottom-dependent animals which perform, with varying amplitude, intensity, and regularity, seasonal or daily vertical migrations above the seabed (Brunel et al. 1978). Hyperbenthos can be distinguished as the permanent hyperbenthos (amphipods, cumaceans, decapods, isopods, mysids, pycnogonids, and tanaids) and near-bottom zooplankton (subdivided into mesozooplankton: copepods, crustacean larvae, chaetognaths, and polychaete larvae; and macrozooplankton: ctenophores and postlarval fishes) (Mees and Jones 1997). Thus, the hyperbenthos comprises a broad assemblage of various organisms related by their distribution in space and not by phylogeny or functional attributes. There are considerable practical difficulties in quantitatively sampling these often highly mobile and small animals. They may be caught occasionally by conventional sampling gears (e.g., grabs, and corers; Eleftheriou and Holme 1984) but are not retained in the net of traditional fisheries assessment gears (Hall 1999). Furthermore, observations of hyperbenthic animals in the stomach contents of predatory fish gives only qualitative information on the presence of these groups of organisms in the benthic environment (Labropoulou and

[1] E-mail: yol72@imbc.gr
[2] E-mail: kdounas@imbc.gr
[3] E-mail: telef@imbc.gr

Eleftheriou 1997). This lack of quantitative information contrasts with the importance of hyperbenthos to fisheries, as the hyperbenthic communities act as a food resource for many commercially exploited demersal fish and epibenthic crustaceans (Carrassón et al. 1997; Martin and Christiansen 1997; Cartes and Maynou 1998).

The aim of this study was to investigate the effects of otter trawling on the hyperbenthic community of the continental shelf of Heraklion Bay (Cretan Sea, Greece, Eastern Mediterranean). The study utilized a new sampling device (Koulouri et al. 2003) that simulates the disturbance of the seabed (and hyperbenthic organisms) caused by the passage of an otter trawl groundrope over the sediment surface.

Methods

Heraklion Bay fishing ground, which occupies an area of 110 km², is located on the northern coast of Crete (Cretan Sea, Greece, Eastern Mediterranean) between 35°20'N and 35°28'N and 25°'02'E and 25°20'E (Figure 1). The experimental site was selected within the fishing ground along the 50-m isobath, which coincides with a traditional fishing lane where most of the local commercial trawling is concentrated. Only one sedimentary facies, mud, is distinguished at the study site (Chronis et al. 2000). Polychaetes are the dominant macrobenthic infaunal group, in terms of species numbers, abundance, and biomass, followed by mollusks and crustaceans (Karakassis and Eleftheriou 1997). The dominant benthopelagic fish species of commercial value are: *Mullus barbatus* Linnaeus 1758, *M. surmuletus* Linnaeus 1758, *Serranus hepatus* (Linnaeus 1758), and *S. cabrilla* (Linnaeus 1758) (Kallianiotis et al. 2000). The commercial trawling season runs from the beginning of October until the end of May. Our field experiments were carried out during daylight hours on two sampling occasions, before (27 September 2001) and a week after (7 October 2001) the beginning of commercial trawling. On both occasions, the experimental site was surveyed with an underwater towed video sledge. Recent trawling activity was evident by fresh marks on the seabed, indicated by hard edges, uncovered lighter-gray sediments, and flat areas with no sedimentary features. Before the beginning of commercial trawling, older marks, indicated by softer edges with numerous bioturbation features such as burrows and mounds, were visible. It should be noted that since the beginning of the trawling season (1 October 2001), two trawlers were observed operating within the experimental site.

The sampling gear constructed and used for the experiment was a modified version of Towed Trawl Simulator Sledge (TTSS2, Dounas et al. 2002; Koulouri et al. 2003) fitted with an otter trawl groundrope (as used by local trawlers) in contact with the seabed (Figure 2). Three nets (0.5-mm mesh size) with three doors attached to a metal frame were added in order to permit sampling of macrobenthic fauna at three levels (5–30 cm, 31–56 m, and 57–82 m) above the sediment surface. An electro-

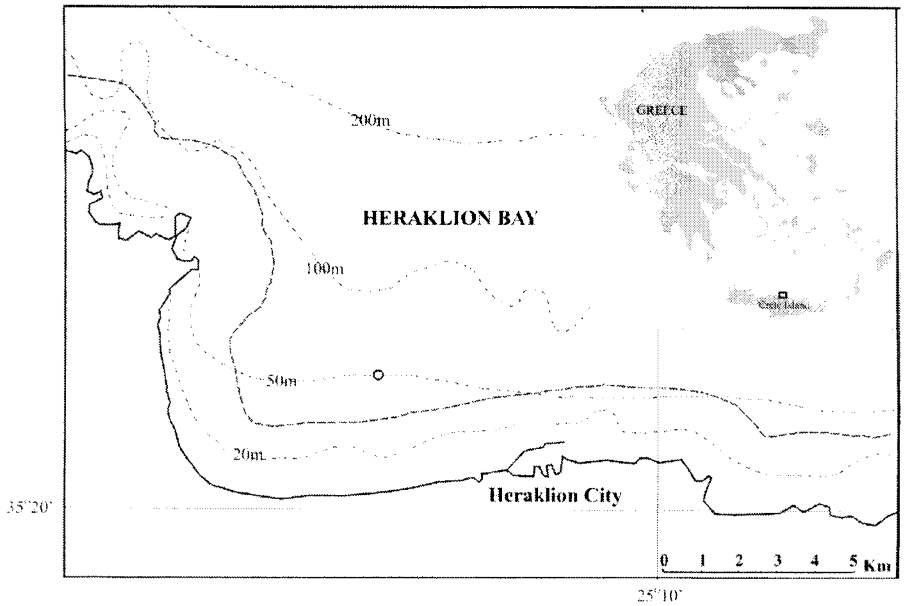

Figure 1. Map of Heraklion Bay (Crete Island, Greece, Eastern Mediterranean) showing the location of the station occupied during this study (bold dashed line shows 1,852-m (1-nautical-mi) trawling limit according to the Greek Fisheries Legislation (i.e., all bottom trawling must occur offshore of this line).

mechanical system allowed the opening (horizontal position) and closing (vertical position) of the three doors simultaneously, and an odometer was used to measure the distance traveled by the gear while in contact with the bottom. The otter trawl groundrope (1.8-m length, 6.5-cm diameter, 2-kg/m weight in water) was supported by two lightweight metal arms attached to the sides of the sledge and was positioned at a distance of 1.5 m in front of the sledge. A video camera attached to the sledge visually covered the performance of the underwater apparatus and showed that resuspension ahead of the sampling nets was caused solely by the groundrope and that the sediment cloud was no higher than the upper sampling net. The sledge was towed by the RV *PHILIA* at a normal trawling speed of ~1 m/second (2 knots). The ratio of length of wire paid out to depth was 2:1.

Profiles of standard hydrographic parameters (temperature, photosynthetically active radiation, chlorophyll a, salinity, density, and dissolved oxygen) were measured in the water column at the 50-m isobath on both sampling occasions using a conductivity/temperature/depth profiler (CTD; SBE-25, Sea-Bird Electronics, Inc., Washington).

Experimental sledge tows during daylight hours were made before and after the beginning of the trawling season. Bearing in mind the homogeneity of the bottom habitat, samples were collected on three disturbed (groundrope present) and three undisturbed (without groundrope) replicate tows along the 50-m isobath on 27 September 2001, prior to the trawling season. No attempt was made to sample exactly on the same positions, and therefore, the sampling can be considered to have been randomly distributed along the trawl track. The experimental site was sampled again (four disturbed and four undisturbed rep-

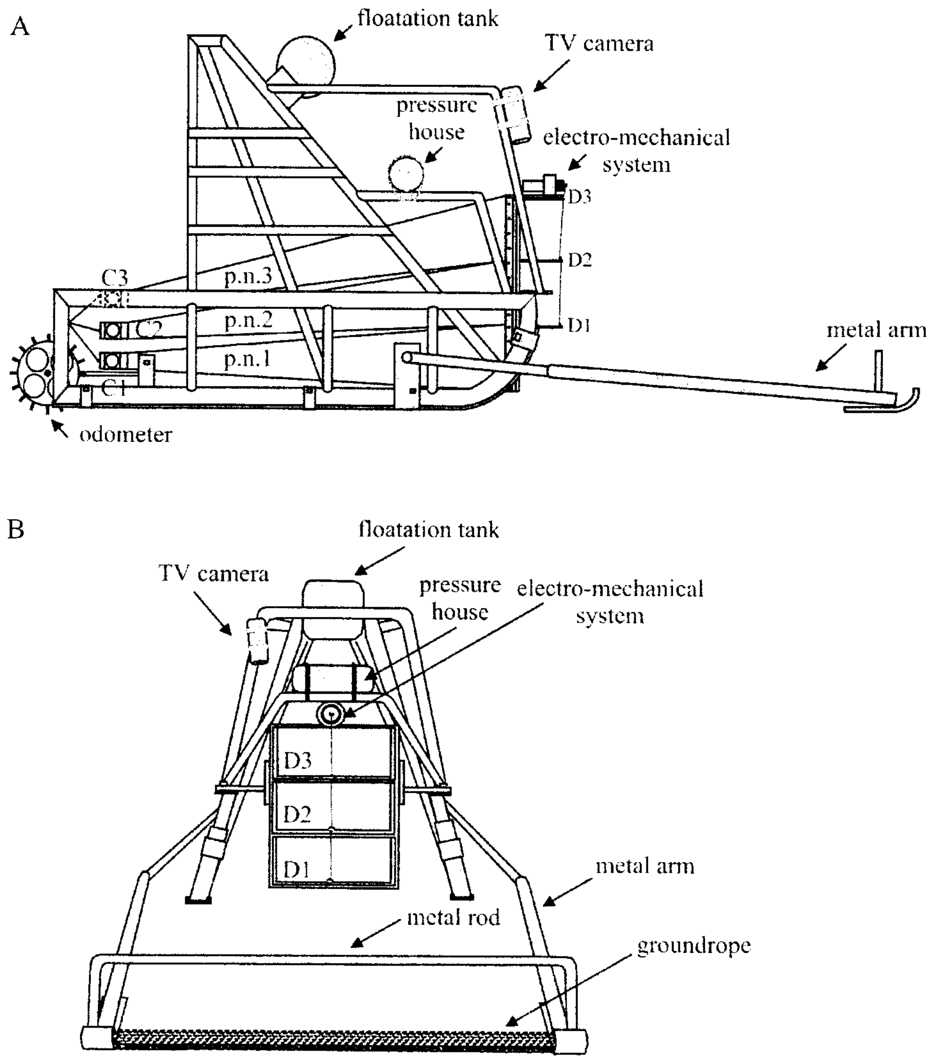

Figure 2. (A) Lateral schematic view of the TTSS2. p.n. = plankton net; C = collectors; D = doors. (B) Front schematic view of the TTSS2 (from Koulouri et al. 2003).

licate tows) on 7 October 2001, after the trawling season had commenced. Material collected was fixed with 10% formalin on board immediately after collection and sorted under a dissecting microscope, and the organisms were identified to the major taxonomic groups and counted for each replicate tow.

Densities of each taxon of the macrofauna were standardized separately to the number of individuals/m^2 of seabed for the three nets in each tow. Densities of the three nets were summed for each experimental sledge tow. Averaged densities of animals from the replicates of disturbed and undisturbed tows before and after the trawling season were calculated. The statistical significance of differences in the densities of the major taxonomic groups was assessed using the Mann–Whitney *U*-test.

In order to investigate the similarity between different tows, cluster analysis was performed using the Bray-Curtis similarity index (Bray and Curtis 1957) and the group average linkage method (Clarke and Warwick 1994). Data for the total number of individuals/m^2 were transformed to the square root prior to analysis. An analysis of similarity test (ANOSIM) was performed to investigate the significance of any differences found (Clarke and Green 1988; Clarke and Warwick 1993). The PRIMER statistical software package (Plymouth Marine Laboratory, Plymouth, UK) was used for the above data analyses.

Results

Data of the hydrographic parameters measured before and after the beginning of the trawling season are similar, indicating relatively stable conditions (Figure 3). No storm event took place during the short period between the two sampling occasions.

A total of 10,065 individuals were identified to 27 major taxa from all the experimental sledge tows. The averaged densities of the major taxa collected from the undisturbed and disturbed sampling tows in both sampling occasions are shown in Tables 1 and 2, respectively. The TTSS2 with groundrope present collected animals from a wide range of taxonomic groups (27), while the TTSS2 without groundrope collected a much smaller number of taxa (13). Gastropoda, Polychaeta, Mysidacea, Amphipoda, and Cumacea were the most abundant groups in the disturbed samples. Comparison of the averaged densities of the major taxa shows that most of the taxonomic groups collected from the disturbed (Table 2) tows were greater than those collected in the undisturbed (Table 1) tows at least by one order of magnitude.

The abundances of several animal groups were lower after the trawling season had commenced, while some others appeared to be higher. The densities of seven disturbed and four undisturbed major taxonomic groups varied sig-

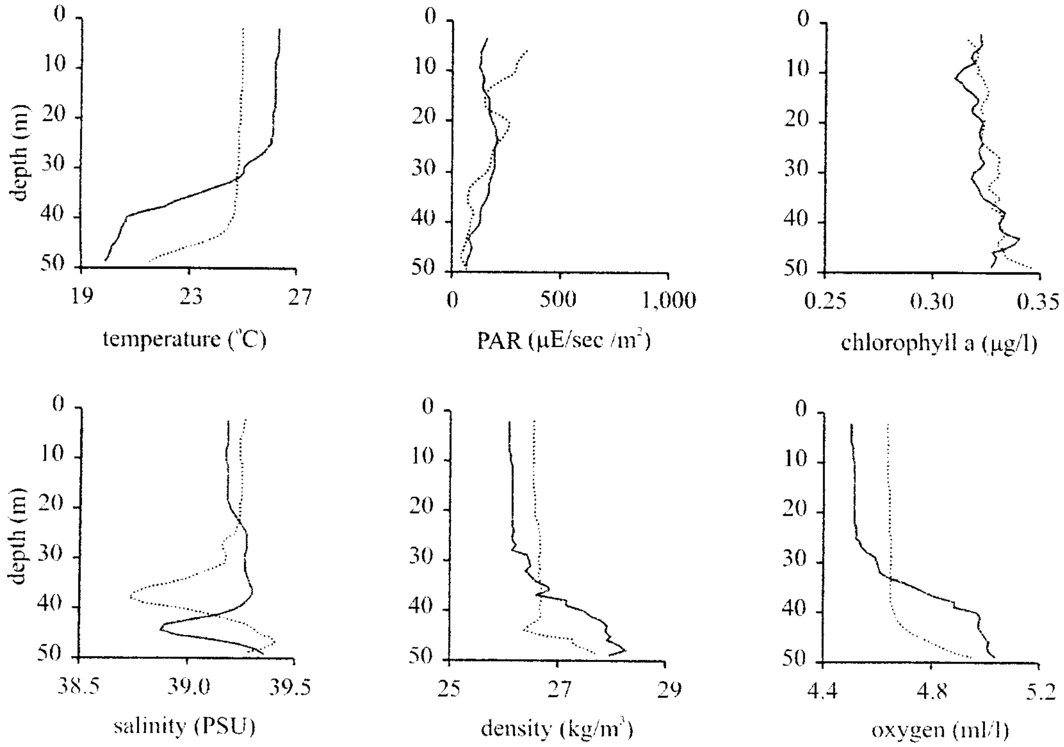

Figure 3. Standard water column hydrographic measurements (temperature, photosynthetically active radiation [PAR], chlorophyll a, salinity, density, oxygen) before (27 September 2001; black line) and after (7 October 2001; dashed line) the beginning of the commercial trawling season in Crete.

Table 1. Averaged densities (individuals/m^2 ± SD) of the major taxa collected from the undisturbed experimental sledge tows before (27 September 2001) and after (7 October 2001) the beginning of the commercial trawling season in Crete (n = number of tows). Statistical significance of differences in densities between the two sampling occasions was determined with Mann-Whitney U-test. n.s. = not significant.

Taxa	Before (n = 3)	After (n = 4)	P
Cnidaria	0.10 ± 0.05	0.03 ± 0.02	n.s.
Crustacea (larvae)	0.52 ± 0.30	0.23 ± 0.05	n.s.
Copepoda	0.11 ± 0.05	0.20 ± 0.05	<0.05
Decapoda	<0.01	<0.01	n.s.
Mysidacea	<0.01	0.02 ± 0.02	n.s.
Cumacea	<0.01	0.03 ± 0.02	<0.05
Isopoda	<0.01	<0.01	n.s.
Amphipoda	0.01 ± 0.01	0.03 ± 0.02	n.s.
Chaetognatha	0.08 ± 0.03	0.07 ± 0.02	n.s.
Echinodermata	0.03 ± 0.02	<0.01	<0.05
Thaliacea	0.04 ± 0.02	<0.01	<0.05
Fish larvae	0.02 ± 0.02	<0.01	n.s.
Eggs	0.01 ± 0.01	0.03 ± 0.02	n.s.

nificantly (Tables 1, 2, $P < 0.05$) between the two sampling occasions. In particular, the average densities of Gastropoda, Bivalvia, and Polychaeta (Figure 4a, 4b, 4c) collected from the disturbed tows decreased significantly after the beginning of the trawling period. On the other hand, the densities of Decapoda, Mysidacea, Amphipoda, and crustacean larvae appeared not to be affected by commercial trawling (Figures 4d, 5a, 5c, 5d). Abundances of Cumacea and Copepoda were significantly greater after the beginning of the trawling season in both disturbed and undisturbed sampling tows (Figures 5b, 5e), while numbers of Chaetognatha increased only in the disturbed tows (Figure 5f).

The similarity dendrogram based on the density matrices of the major taxonomic groups (Figure 6) showed a clear separation of the samples from disturbed and undisturbed tows comprising two major groups. Furthermore, within each group of tows, the two sampling occasions were also separated in two distinct subgroups, indicating that the benthic community has been altered, probably as a result of commercial trawling activity in the area. The results of the ANOSIM test revealed that the above four groups of tows were significantly different.

Discussion

It has been suggested that the impact of otter trawling is largely restricted to the disturbance caused by the doors (Hall 1999). However, the effect of the groundrope in a trawling rig should not be underestimated, as it accounts

Table 2. Averaged densities (individuals/m^2 ± SD) of the major taxa collected from the disturbed experimental sledge tows before (27 September 2001) and after (7 October 2001) the beginning of the commercial trawling season in Crete (n = number of tows). Statistical significance of differences in densities between the two sampling occasions was determined with Mann-Whitney U-test. n.s. = not significant.

Taxa	Before (n = 3)	After (n = 4)	P
Porifera	0.01 ± 0.02	0.02 ± 0.04	n.s.
Cnidaria	0.08 ± 0.07	0.41 ± 0.17	<0.05
Ctenophora		<0.01	n.s.
Nemertini	0.02 ± 0.02		n.s.
Sipuncula	0.10 ± 0.12	0.01 ± 0.02	n.s.
Gastropoda	6.25 ± 1.37	1.12 ± 0.71	<0.05
Scaphopoda		0.09 ± 0.12	n.s.
Bivalvia	1.05 ± 0.19	0.60 ± 0.21	<0.05
Polychaeta	3.43 ± 0.38	1.43 ± 0.57	<0.05
Crustacea (larvae)	2.91 ± 0.65	3.65 ±1.59	n.s.
Copepoda	0.36 ± 0.12	3.17 ± 0.59	<0.05
Ostracoda	0.33 ± 0.33	0.10 ± 0.07	n.s.
Decapoda	1.53 ± 0.40	1.82 ± 1.24	n.s.
Mysidacea	10.55 ± 1.53	6.82 ± 3.15	n.s.
Cumacea	4.33 ± 1.66	7.38 ± 1.64	<0.05
Tanaidacea	0.01 ± 0.02	0.02 ± 0.03	n.s.
Isopoda	0.21 ± 0.12	0.21 ± 0.10	n.s.
Amphipoda	5.77 ± 1.10	5.67 ± 1.67	n.s.
Pycnogonida	0.08 ± 0.07	0.06 ± 0.06	n.s.
Chaetognatha	0.76 ± 0.27	1.37 ± 0.29	<0.05
Echinodermata	1.22 ± 0.50	0.44 ± 0.28	n.s.
Appendicularia	0.07 ± 0.09	0.02 ± 0.02	n.s.
Ascidiacea	<0.01		n.s.
Thaliacea	0.01 ± 0.02	0.03 ± 0.03	n.s.
Fish larvae	0.10 ± 0.06	0.09 ± 0.07	n.s.
Pisces	0.03 ± 0.03	0.05 ± 0.03	n.s.
Eggs	0.28 ± 0.12	0.13 ± 0.06	n.s.

usually for more than 90% of the area of contact of the trawl gear with the seabed (Lindeboom and de Groot 1998). The groundrope used in these experiments penetrated the muddy sediment of Heraklion Bay less than 1 mm (Dounas et al. 2002). Observations made on the Heraklion Bay fishing grounds using the new TTSS2 sampling gear to simulate sediment disturbance by otter trawl groundrope showed significant perturbations of small-sized benthos living on or very close to the sediment–water interface.

Hyperbenthic sampling (TTSS2 without groundrope) in the study area revealed low activity of animals above the seabed. Most hyperbenthic species seem to be very closely associated with the sediment during the day, undertaking vertical migrations during darkness (Sainte-Marie and Brunel 1983, 1985; Kaartvedt 1986). However, sediment disturbance experiments using the

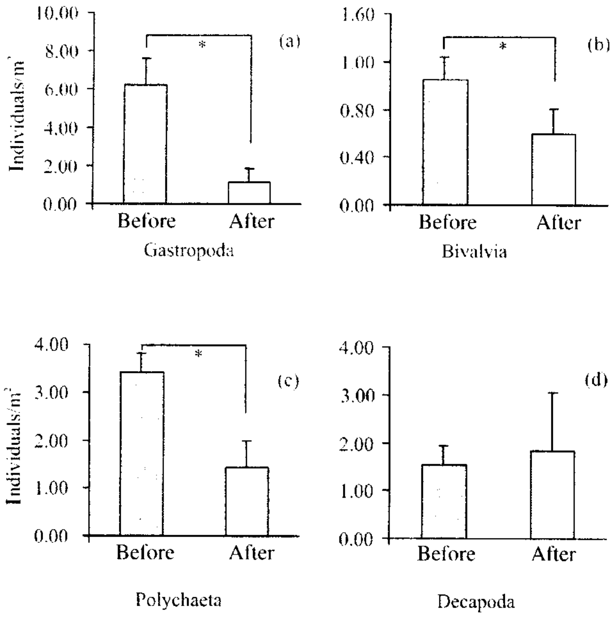

Figure 4. Averaged densities (individuals/m² ± SD) of four major epibenthic taxa collected from the "disturbed" tows before and after the beginning of the commercial trawling season. An asterisk indicates that statistically significant differences were determined by the Mann–Whitney *U*-test ($P < 0.05$).

TTSS2 and the otter trawl groundrope disturbed not only a large number of epibenthic animals but also rich hyperbenthic and zooplanktonic fauna living on or a few centimeters above the bottom during daylight.

Changes observed in the abundance of certain taxonomic groups a week after the start of the trawling period in the area cannot be attributed to any natural disturbance event, as calm weather conditions prevailed throughout the sampling period. This is consistent with the similarity between the hydrographic conditions measured on the two sampling occasions.

A large number of benthic animals may have been displaced, damaged, or killed by the passage of trawl gear, generating a food source for predators and scavengers (Britton and Morton 1994; Kaiser and Ramsay 1997; Groenewold and Fonds 2000). Hence, it was not unexpected to observe significant decreases in the abundance of the major epibenthic groups such as gastropods, bivalves, and polychetes shortly after the beginning of the trawling season. On the contrary, the densities of some hyperbenthic and zooplanktonic groups, such as cumaceans, copepods, and chaetognaths, increased markedly. These increases probably were due to immigration of animals from the neighboring untrawled

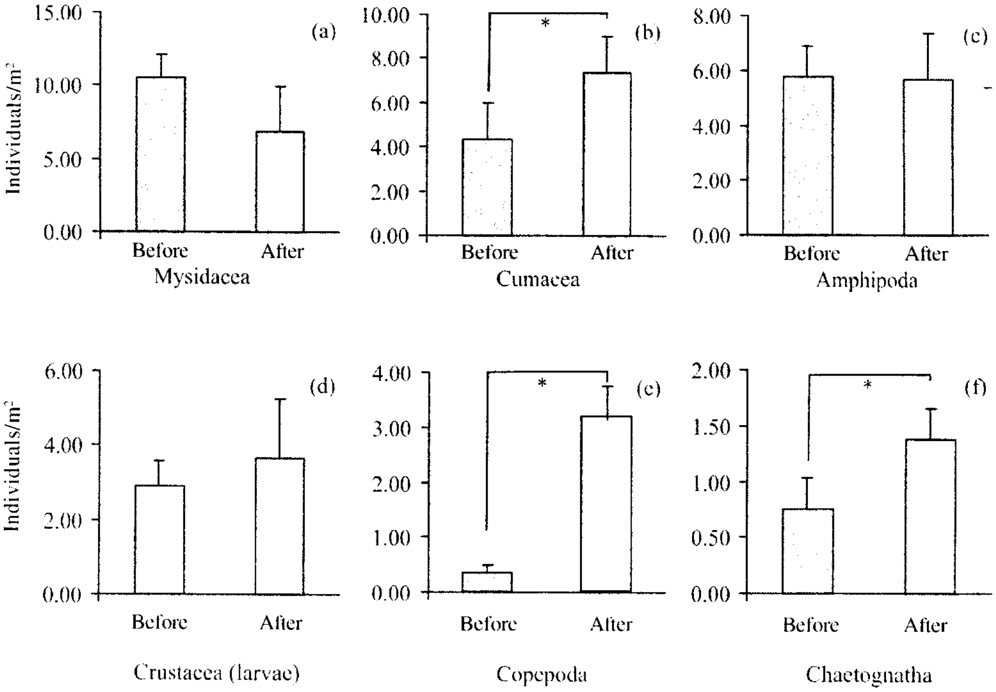

Figure 5. Averaged densities (individuals/m² ± SD) of six major hyperbenthic (a, b, c) and zooplanktonic (d, e, f) taxonomic groups collected from the "disturbed" tows before and after the beginning of the commercial trawling season. An asterisk indicates that statistically significant differences were determined by the Mann–Whitney *U*-test ($P < 0.05$).

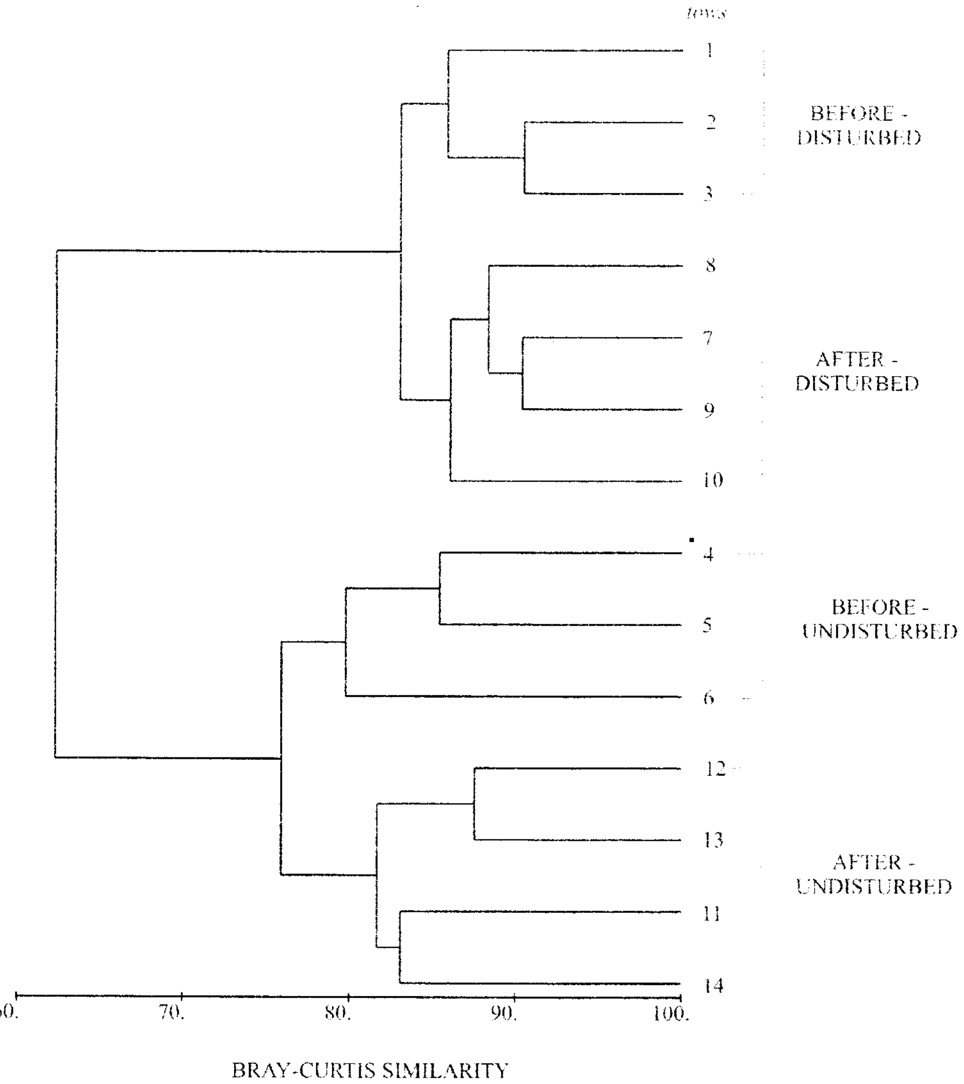

Figure 6. Similarity dendrogram based on density matrices of the major taxa collected from the "undisturbed" and "disturbed" tows before and after the beginning of the commercial trawling season. Statistical significance of differences among the four groups of tows was determined with an ANOSIM test (R = 0.861; P < 0.001).

areas into the fishing ground where there is increased availability of food and to the removal of large predators by the fishing gear (Kaiser and Spencer 1994; Ramsay et al. 1997; Prena et al. 1999). Other groups, such as decapods, mysids, amphipods, and crustacean larvae, appeared to be unaffected, although they also may be attracted by the increased availability of food resource caused by trawling, but they were probably also more vulnerable to predatory pressure from demersal benthivorous fish (Labropoulou and Eleftheriou 1997).

Current knowledge does not allow the prediction of the long-term effects resulting from groundrope disturbance on the epibenthic, the hyperbenthic, or even the zooplanktonic community. The development of novel direct sampling techniques (such as TTSS2) may assist in overcoming problems related to the inaccessibility of the hyperbenthos, which cannot be performed by standard sampling equipment. Ongoing research in the area using TTSS2 combined with conventional benthic and pelagic sampling and stomach content analyses of benthopelagic fish is expected to give further information on the effects of otter trawling on small invertebrates and on the resulting ecosystem responses.

Acknowledgments

This work was carried out in the framework of the project "Development of a new method for the quantitative measurement of the effects of otter trawling on benthic nutrient fluxes and sediment biogeochemistry," which was financed by the European Commission (Directorate General XIV, Studies for the Support of Common Fisheries Policy). The authors acknowledge the technical support provided by the captain and the crew of R/V *PHILIA*. We are also grateful for comments on the manuscript made by C. Arvanitidis.

References

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:220–249.

Britton, J. C., and B. Morton. 1994. Marine carrion and scavengers. Oceanography and Marine Biology: An Annual Review 32:369–434.

Brunel, P., M. Besner, D. Messier, L. Poirier, D. Granger, and M. Weinstein. 1978. Le traîneau suprabenthique Macer-GIROQ: appareil amélioré pour l' échantillonage quantitatif étagé de la petite faune nageuse au voisinage du fond. Internationale Revue der Gesampten Hydrobiologie 63:815–829.

Carrassón, M., J. Matallanas, and M. Casadevall. 1997. Feeding strategies of deep-water morids on the western Mediterranean slope. Deep-Sea Research I 44:1685–1699.

Cartes, J. E., and F. Maynou. 1998. Food consumption by bathyal decapod crustacean assemblages in the western Mediterranean: predatory impact of megafauna and the food consumption-food supply balance in a deep-water food web. Marine Ecology Progress Series 171:233–246.

Chronis, G., V. Lykousis, C. Anagnostou, A. Karageorgis, S. Stavrakakis, and S. Poulos. 2000. Suspended particulate matter and nepheloid layers over the southern margin of the Cretan Sea (N. E. Mediterranean): seasonal distribution and dynamics Progress in Oceanography 46:143–162.

Clarke, K. R., and R. H. Green. 1988. Statistical design and analysis for a "biological effects" study. Marine Ecology Progress Series 46:213–226.

Clarke, K. R., and R. M. Warwick. 1993. Similarity-based testing for community pattern: the 2-way layout with no replication. Marine Biology 118:167–176.

Clarke, K. R., and R. M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth, UK.

Dounas, C., I. Davies, P. Hayes, C. Arvanitidis, and P. Koulouri. 2002. Development of a new method for the quantitative measurement of the effects of otter trawling on benthic nutrient fluxes and sediment biogeochemistry. European Commission, Study Project 99/036, Final Report, Hellenic Centre for Marine Research, Crete, Greece.

Eleftheriou, A., and N. A. Holme. 1984. Macrofauna techniques. Pages 140–216 *in* N. A. Holme and A. D. McIntyre, editors. Methods for the study of marine benthos. Blackwell Scientific Publications, Oxford, UK.

Groenewold, S., and M. Fonds. 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES Journal of Marine Science 57:1395–1406.

Hall, S. J. 1999. The effects of fishing on marine ecosystems and communities. Blackwell Scientific Publications, Oxford, UK.

Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology 34:201–352.

Kaartvedt, S. 1986. Diel activity patterns in deep-living cumaceans and amphipods. Marine Ecology Progress Series 30:243–249.

Kaiser, M. J., and S. J. de Groot. 2000. The effects of fishing on non-target species and habitats. Blackwell Scientific Publications, Oxford, UK.

Kaiser, M. J., and K. Ramsay. 1997. Opportunistic feeding by dabs within areas of trawl disturbance: possible implications for increased survival. Marine Ecology Progress Series 152:307–310.

Kaiser, M. J., and B. E. Spencer. 1994. Fish scavenging behaviour in recently trawled areas. Marine Ecology Progress Series 112:41–49.

Kallianiotis, A., K. Sophronidis, P. Vidoris, and A. Tselepides. 2000. Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): seasonal variation in species density, biomass and diversity. Progress in Oceanography 46:429–455.

Karakassis, I., and A. Eleftheriou. 1997. The continental shelf of Crete: structure of macrobenthic communities. Marine Ecology Progress Series 160:185–196.

Koulouri, P., C. Dounas, and A. Eleftheriou. 2003. A new apparatus for the direct measurement of otter trawling effects on the epibenthic and hyperbenthic macrofauna. Journal of the Marine Biological Association of the United Kingdom 83:1363–1368.

Labropoulou, M., and A. Eleftheriou. 1997. The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. Journal of Fish Biology 50:324–340.

Lindeboom, H. J., and S. J. de Groot. 1998. Impact II. The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. Netherland Institute for Sea Research, NIOZ-Rapport 1998–1/RIVO-DLO Report C003/98, Texel, The Netherlands.

Martin, B., and B. Christiansen. 1997. Diets and standing stocks of benthopelagic fishes at two bathymetrically different midoceanic localities in the northeast Atlantic. Deep-Sea Research I 44:541–558.

Mees, J., and M. B. Jones. 1997. The hyperbenthos. Oceanography and Marine Biology: An Annual Review 35:221–255.

Prena, J., P. Schwinghamer, T. W. Rowell, D. C. Gordon, Jr., K. D. Gilkinson, W. P. Vass, and D. L. McKeown. 1999. Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: analysis of trawl bycatch and effects on epifauna. Marine Ecology Progress Series 181:107–124.

Ramsay, K., M. J. Kaiser, P. G. Moore, and R. N. Hughes.

1997. Consumption of fisheries discards by benthic scavengers: utilization of energy subsidies in different marine habitats. Journal of Animal Ecology 66:884–896.

Sainte-Marie, B., and P. Brunel. 1983. Differences in life history and success between suprabenthic shelf populations of *Arrhis phyllonyx* (Amphipoda, Gammaridea) in tow ecosystems of the Gulf of St. Lawrence. Journal of Crustacean Biology 3:45–69.

Sainte-Marie, B., and P. Brunel. 1985. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of Saint Lawrence. Marine Ecology Progress Series 23:57–69.