

Desperately Searching for Natural Eutrophication: the Case of the NE Mediterranean

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ABSTRACT

In the present work, we review and analyse the major features of the Greek marine fisheries (catch species composition and densities) for the 1982-1989 period and the results are discussed in the context of the trophic potential of the Greek seas (phytoplankton and zooplankton productivity and abundance) and compared with those of other upwelling and non-upwelling areas of the world ocean. Multivariate analyses (classification and ordination) performed on the mean (1982-1989) commercial catch weight of 66 species (or groups of species) from 16 fishing subareas indicated that the 16 subareas fall into three main groups, generally representing the S-SE Aegean (and NW Levantine Seas), the Ionian and central Aegean Seas, and the N-NW Aegean Sea, respectively. The species compositions of the mean catches of the groups identified by multivariate analyses differed considerably. The mean catch of S-SE Aegean was dominated by pickerel and bogue and, to a lesser extent, by horse mackerels, that of the central Aegean and Ionian Seas by sardine, horse mackerel, bogue and pickerel, whereas that of N-NW Aegean Sea by anchovy and sardine. The mean pelagic, demersal and total fisheries catch densities between 1982 to 1989 all decrease from 1.3, 0.83 and 2.13 t/km² in N-NW Aegean Sea to 0.25, 0.37 and 1.23 t/km² in S-SE Aegean Sea, respectively, with the latter densities being comparable to those in the Ionian Sea. In addition, such an increase goes along with

a decrease in the relative importance of demersal species. The mean pelagic catch density in the Ionian and S-SE Aegean Seas is from 3 to 150 times lower than those in other marine areas of the world ocean. In contrast, the mean pelagic catch density in the N-NW Aegean Sea is: (a) comparable to that in the California coast (22-38°N), (b) higher than those in the Gulf of California and Indian waters (7-25°N) and (c) 2 to 30 times lower than those in the major upwelling areas of the world. Natural eutrophication processes are responsible for such a geographical differentiation in catch species composition and densities, namely the gradient in eutrophy, river runoff, temperature and salinity of the Greek marine waters along a NNW to SSE axis. In contrast to other areas where seasonal upwelling takes place (e.g., Ivorian and Ghanaian coasts), seasonal upwelling along the E Aegean coast, driven by the Etesian winds (dry and cool N-NE-E winds blowing over the Aegean Sea in summertime) probably has no significant impact on primary production and fisheries catch densities, most probably because upwelled waters reach the surface from layers immediately below the seasonal thermocline, its depth in the E Aegean Sea generally being <50 m, and, hence, are already poor in nutrients.

RÉSUMÉ

Dans ce travail, nous analysons les principales caractéristiques des pêcheries marines grecques (composition des captures et densités) pour la période 1982-1989 ; les résultats sont discutés en termes de potentiel trophique des eaux maritimes grecques (abondance et productivité du phytoplancton et du zooplancton) et comparés à ceux obtenus dans d'autres zones (d'upwelling ou non). Des analyses multivariées (classification et hiérarchisation) sont faites sur les captures commerciales moyennes de 66 espèces (ou groupes d'espèces) de 16 zones de pêche appartenant à trois groupes : la zone S-SE de la mer Egée (et NW de la mer du Levantin), la mer Ionienne et la zone centrale de la mer Egée, et le N-NW de la mer Egée. La composition des captures diffère beaucoup d'une zone à l'autre. La capture moyenne de la zone S-SE de la mer Egée est dominée par les brochets et les bogues et, dans une moindre mesure, par les chinchards ; celle de la partie centrale de la mer Egée et de la mer Ionienne par les sardines, les chinchards, les bogues et les brochets ; et celle de la zone N-NW de la mer Egée par les anchois et les sardines. Les densités moyennes des captures de poissons pélagiques, démersaux et des captures totales diminuent entre 1982 et 1989 de 1.3, 0.83 et 2.13 t/km² respectivement dans le N-NW de la mer Egée, à 0.25,

0.37 et 1.23 t/km² dans le S-SE de la mer Egée, ces dernières valeurs se retrouvent aussi dans la mer Ionienne. De plus, un tel accroissement va de pair avec une décroissance de l'importance relative dans chacune des zones des espèces démersales. La densité des captures de poissons pélagiques dans la mer Ionienne et dans le S-SE de la mer Egée est de 3 à 150 fois plus faible que celle d'autres zones marines. Par exemple, la capture moyenne des pélagiques dans le N-NW de la mer Egée est (a) comparable à celle de la Californie (22-38 °N), (b) plus importante que celle du golfe de Californie et de l'Inde (7-25 °N) et (c) de 2 à 30 fois plus faible que celle des principales zones d'upwelling mondiales. Les processus d'eutrophisation naturelle que sont le gradient d'eutrophisation, le débit des rivières, la température, la salinité des eaux le long de l'axe N-NW à S-SE, sont responsables de ces différences de composition des captures et des densités. Par comparaison avec les autres upwellings saisonniers d'autres zones (par exemple Côte-d'Ivoire-Ghana), celui des côtes orientales de la mer Egée, soumis aux vents Etésiens secs et froids, N-NE-E, qui soufflent sur la mer Egée en été, n'a probablement pas d'impact sur la production primaire et sur les captures. Les eaux upwellées atteignent la surface depuis des couches situées juste en dessous de la thermocline dont la profondeur dans l'est de la mer Egée est généralement inférieure à 50 m. De ce fait, elles sont généralement pauvres en sels nutritifs.

INTRODUCTION

The Mediterranean Sea has a maximal depth of 5 140 m, maximal width of 800 km, an area of 2.5 million km² (0.8% of the total marine area of the world) and a mean depth of 1 470 m (Azov, 1991). There is a pronounced oligotrophy in the surface waters of the Mediterranean Sea, especially so in its eastern part (Aegean and Levantine Seas). The lack of significant upwelling areas resulting from upwelling of 'new' nutrients from deep waters in the euphotic zone, an important key to high biological productivity, and the relatively small amounts of discharge from land, results in low nutrient concentration in the trophogenic layer. In addition, the Mediterranean Sea is a concentration basin in which total evaporation exceeds precipitation and river runoff (Hopkins, 1978) and the conservation of mass and salinity is maintained by the balance of the two-layer flow through the Strait of Gibraltar: surface, nutrient-poor Atlantic waters inflowing in the upper layer and Mediterranean deeper waters outflowing in the lower layer. The low concentration of phosphates in deeper waters, reflect the restricted exchange of the landlocked water with the waters of the adjacent Atlantic Ocean. The oligotrophy of the Mediterranean Sea is also reflected in the level of fisheries catches (300 kg/km² for all areas and 1,400 kg/km² over the continental shelf, Ben Tuvia, 1983).

The marine waters of Greece include the Aegean Sea and a part of the Ionian and NW Levantine Seas. The Greek part of the Ionian Sea comprises a part of a larger area in which the existing stocks are fished by a number of other major fishing nations (especially Albania, Italy, Libya, Malta and Tunisia). The mean Greek catch from the Ionian Sea over the period 1982-1987 represented only 7% of the total Ionian Sea catch (FAO, 1989). The Greek part of the Levantine Sea also comprises a part of a larger area in which the existing stocks are fished by a number of other major fishing nations (Lebanon, Turkey, Israel, Syria, Cyprus, Egypt and Gaza Strip). The mean Greek catch from the NW Levantine Sea over the period 1982-1987 represented less than 1% of the total Levantine catch. In contrast, the Aegean Sea is mainly fished by the Greek fleet. Although the Turkish fleet fishes along the eastern Aegean coast, the Turkish catch from this area is relatively insignificant when compared with that of the Greek Aegean Sea fisheries; it comprised about 20% of the mean total Aegean catch over the period 1982-1987 (FAO, 1989).

In the present work, we analyse the major aspects of the Greek marine fisheries (catch species composition and density) for the 1982-1989 period. The results are discussed in the context of the trophic potential of the Greek Seas (phytoplankton and zooplankton productivity and abundance) and compared with those of other upwelling and non-upwelling areas of the world ocean.

1. MATERIAL AND METHODS

Fisheries statistics for the waters of Greece have been recorded on a monthly basis since January 1964 by the National Statistical Service of Hellas (NSSH Bulletins, 1965-1990). For a better evaluation of the available data, the waters fished by Greek vessels have been divided into 18 statistical fishing subareas (Fig. 1). Fishing subareas 1 and 2 (not shown in Fig. 1) refer to the Atlantic Ocean and the northern coast of Africa, respectively. Catch data are collected directly from a sample of fishing vessels (stratified random sampling) that are surveyed by local customs authorities. For each vessel surveyed, a statistical questionnaire is completed showing the quantities of each major fish species (or group of species) caught during the previous month (or that the vessel did not work during that period). Details on the validity of the NSSH data have been presented by Stergiou *et al.* (1994).

In general, the Greek fishing fleet includes: (a) fishing vessels operating in distant waters (Atlantic Ocean and northern African coast, and thus of no concern to the present study); (b) trawlers operating in Greek open-sea waters; (c) purse seiners operating in Greek open-sea and coastal waters; (d) beach seiners operating along the Greek coasts; and (e) 'other coastal boats' (including small ring netters, drifters, liners, etc.) operating along the Greek coasts. Since 1969 the catches of the smaller inshore ring netters, drifters and liners (i.e., boats with engine horsepower of less than 20HP) have not been recorded by the local customs authorities. In addition, the catches from the marine sport fisheries, which locally may be relatively important (e.g., 11.8% and 4.5% of the total catches from subareas 9 and 5, respectively; Stergiou *et al.*, 1989) are not included in the totals.

For the period 1964-1981, separate catch statistics are available for 23 species or groups of species only whereas for the years following 1981 separate catch statistics have been available for 66 species (or groups of species) of commercially important fishes, cephalopods and crustaceans (Stergiou *et al.*, 1994). In the present study, the annual landed catches of the 66 species (or groups of species) in the 16 statistical fishing subareas (Fig. 1) for the years 1982-1989 inclusive, were analysed using two main categories of statistical techniques, as follows.

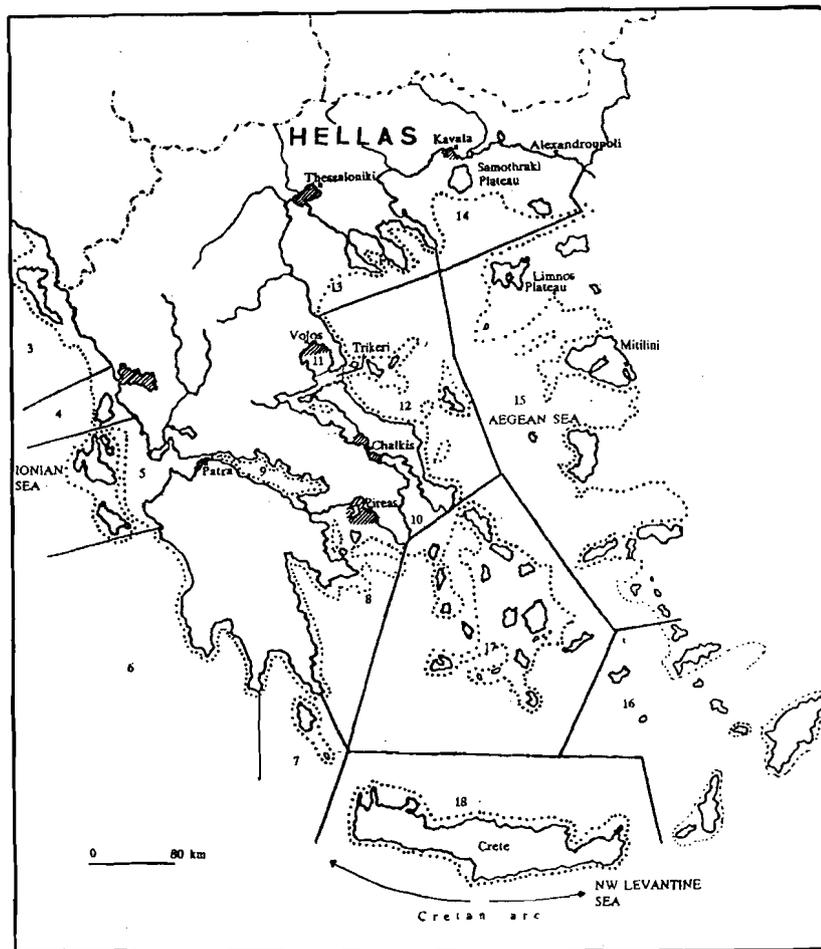


Fig. 1: Map showing the 16 fishing subareas of Greece (Hellas). The dotted line represents the 200 m isobath; hatchings show areas where anthropogenic eutrophication is locally important.

The following univariate measures were computed: mean number of species, species diversity, richness and evenness for each subarea over the 1982-1989 period. Diversity was calculated using the Shannon-Wiener diversity index H' , species richness using Margalef's D , and evenness using Pielou's J (Magurán, 1988). All computations were carried out using the PRIMER algorithms (Clarke and Warwick, 1989).

A matrix comprising the mean landed commercial catch weight of each species (or groups of species) from each subarea over the 1982-1989 period was compiled. From that matrix, a triangular matrix of similarities between all pairs of subareas was computed using the Bray-Curtis coefficient (Bray and Curtis, 1957). Prior to this computation, the data was standardized by the mean total landed catch per subarea in order to compensate for between-subarea differences in fishing effort, for which data per subarea is not provided in the NSSH Bulletins. Subsequently, the similarity matrices were subjected to both clustering (employing group-average linking) and ordination (employing non-metric multi-dimensional

scaling, MDS) analysis techniques. The adequacy of the ordination in two, rather than more than two, dimensions is expressed by a 'stress coefficient' (Field *et al.*, 1982). In general, stress values <0.1 imply good representation (Clarke and Warwick, 1989). Discontinuities between subareas may be accepted as real when the results of the two methods agree (Field *et al.*, 1982; Clarke and Green, 1988; Gray *et al.*, 1988). All multivariate analyses were carried out using the PRIMER algorithms (Clarke and Warwick, 1989).

2. RESULTS

Overall, the two pelagic species anchovy and sardine were dominant, comprising 18.5% and 11.4% of the mean total Greek catch, respectively, over the 1982-1989 period (Fig. 2). In addition, bogue, horse mackerel, pickerel, hake and chub mackerel comprised 8.2%, 8.0%, 7.3%, 3.3% and 3.3% of the mean catch, respectively (Fig. 2). All remaining species each contributed less than 3%. However, catch species composition differs greatly between fishing subareas and component fisheries.

The species composition of the mean catch per component fishery over the 1982-1987 period is shown in Table 1. The mean trawl catch was dominated by hake, pickerel, horse mackerel and red mullet; the mean purse seine catch mainly by anchovy and, to a lesser degree, by sardine, horse mackerel and bogue; the mean beach seine catch mainly by pickerel and, to a lesser degree, by sardine and bogue; and, finally, the mean 'other coastal boats' catch by bogue, pickerel and grey mullets.

The mean annual commercial catch weights per fishing subarea over the 1982-1989 period are shown in Table 2. The mean annual Greek catch was 92 841 t, of which 86 584 t were caught in the Aegean Sea (less than 1% was derived from the NW Levantine Sea) and 6 257 t in the Ionian Sea. Fish made up 94.2% of the mean total Aegean catch, cephalopods 3.2% and crustaceans 2.6%. In the Ionian Sea, fish made up 95.7% of the mean total catch, cephalopods 3.2% and crustaceans 1.1%.

The mean annual catch weight, mean number of species comprising the catch, and the mean diversity (Shannon-Wiener diversity, evenness and richness) over the 16 fishing subareas are shown in Table 3. The total number of species ranged from 56 (in subarea 6) to 66 (in subareas 8, 10 and 12 to 16). Richness ranged between 6.39 (in subarea 13) and 12.05 (in subarea 6), diversity between 1.67 (in subarea 11) and 3.38 (in subarea 6) and evenness between 0.41 (in subarea 11) and 0.84 (in subarea 6). The following significant regression was found between the log-transformed mean catch weights (C) and number of species (N) comprising mean catches for each subarea over the 1982-1989 period: $\text{Ln}(C) = -92.83 + 24.25\text{Ln}(N)$, $\text{SE}(\text{slope})=3.75$, $r^2=0.75$, $n=16$, $P<0.01$.

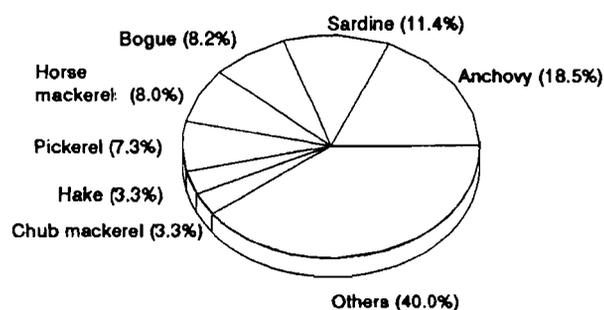


Fig. 2: Species composition of the mean total Greek marine catch, 1982-1989, in % of total weight.

Common name	Scientific name	T	P	S	O
FISHES					
Anchovy	<i>Engraulis encrasicolus</i> (L.)	1.9	95.4	0.9	1.8
Anglerfish	<i>Lophius</i> spp.	94.9	0.4	0.6	4.0
Annular sea bream	<i>Diplodus annularis</i> (L.)	8.8	13.3	0.8	77.1
Black sea bream	<i>Spondylisoma cantharus</i> (L.)	13.7	6.8	6.0	73.6
Blotched pickarel	<i>Spicara flexuosa</i> Rafinesque, 1810	49.5	7.6	11.6	31.2
Blue whiting	<i>Micromesistius poutassou</i> (Risso, 1826)	93.8	0.5	3.3	2.4
Bluefin tuna	<i>Thunnus thynnus</i> (L.)	0.3	39.7	0.6	59.4
Bluefish	<i>Pomatomus saltator</i> (L.)	6.0	36.5	2.0	55.5
Bogue	<i>Boops boops</i> (L.)	11.0	51.8	11.8	25.4
Bonito	<i>Sarda sarda</i> (Bloch, 1793)	1.4	64.5	2.1	32.0
Brill	<i>Scophthalmus rhombus</i> (L.)	83.4	2.8	0.2	13.6
Chub mackerel	<i>Scomber japonicus</i> (Houttuyn, 1782)	3.3	82.7	3.8	10.3
Comber	<i>Serranus cabrilla</i> (L.)	32.6	5.8	2.1	59.6
Common dentex	<i>Dentex dentex</i> (L.)	9.3	2.6	5.3	82.8
Common sea bream	<i>Pagrus pagrus</i> (L.)	6.9	1.7	2.1	89.2
Dogfishes	Squalidae	37.0	4.3	0.6	58.1
Dusky grouper	<i>Epinephelus guaza</i> (L.)	3.5	5.2	1.5	89.8
European eel	<i>Anguilla anguilla</i> (L.)	2.2	5.1	0.7	92.0
European sardine	<i>Sardina pilchardus</i> (Walbaum, 1792)	1.7	77.9	9.0	11.4
European sea bass	<i>Dicentrarchus labrax</i> (L.)	24.6	14.4	3.0	58.0
Griffish	<i>Belone belone gracilis</i> (Lowe, 1839)	0.9	11.3	10.3	77.5
Gilt sardine	<i>Alosa falax nilotica</i> (Geoffroy Saint-Hilaire, 1808) and <i>Sardinella aurita</i> (Valenciennes, 1847)	5.4	70.2	2.1	22.2
Gilthead sea bream	<i>Sparus aurata</i> L.	71.6	7.8	2.8	17.8
Greater amberjack	<i>Seriola dumerli</i> (Risso, 1810)	21.5	24.0	4.0	50.5
Grey mullet	Mugilidae	9.5	17.3	0.7	72.5
Guitarfish	<i>Rhinobatos</i> spp.	65.5	1.1	4.7	28.7
Gurnard	Triglidae	35.4	0.8	8.6	55.2
Hake	<i>Mertuicius merluccius</i> (L.)	69.4	3.9	2.0	24.7
Horse mackerels	<i>Trachurus</i> spp.	17.3	67.7	4.0	11.0
Jack mackerel	<i>Trachurus picturatus</i> (Bowdich, 1825)	23.4	67.7	4.4	4.5
John dory	<i>Zeus faber</i> (L.)	79.6	0.8	3.8	15.8
Large-eye dentex	<i>Dentex macrophthalmus</i> (Bloch, 1791)	51.4	2.3	4.9	41.4
Mackerel	<i>Scomber scombrus</i> (L.)	7.9	60.3	2.9	28.8
Pickarel	<i>Spicara smaris</i> (L.)	22.2	9.0	45.5	23.3
Rays	<i>Raja</i> spp.	88.0	0.2	0.4	11.3
Red mullet	<i>Mullus barbatus</i> (L.)	72.6	3.1	5.2	19.1
Red pandora	<i>Pagellus erythrinus</i> (L.)	53.0	1.9	5.3	39.8
Rockfish	<i>Helicolenus dactylopterus</i> (Delaroche, 1809)	66.6	3.1	4.7	25.7
Saddled bream	<i>Oblada melanura</i> (L.)	12.4	17.3	4.0	66.4
Salema	<i>Sarpa salpa</i> (L.)	4.9	24.5	3.1	67.5

Table 1: Common names, scientific names and percentages of mean annual total catches of the 66 species (or groups of species), recorded by the Greek National Statistical Service, fished by trawlers (T), purse seiners (P), beach seiners (S) and 'other coastal boats' (= small ring netters, liners, drifters, etc.; O) over the period 1982-1987. Species are listed in alphabetical order with respect to common name. Sum across lines is 100% (from Sergiou and Pollard, in press).

Common name	Scientific name	T	P	S	O
BONY FISH					
Scorpionfish	<i>Scorpaena</i> spp.	24.7	4.4	2.7	68.3
Shi drum	<i>Umbrina cirrosa</i> (L.)	33.5	4.7	1.5	60.3
Skipjack	<i>Katsuwonus pelamis</i> (L.)	2.4	76.4	1.9	19.4
Smoothhound	<i>Mustellus</i> spp.	38.1	36.5	0.5	24.9
Sole	<i>Soleidae</i> (mainly <i>Solea vulgaris</i> Quensel, 1806)	13.5	3.4	0.5	82.7
Sprat	<i>Sprattus sprattus</i> (L.)	9.5	68.8	4.4	17.3
Stone bass	<i>Polyprion americanus</i> (Schneider, 1801)	4.5	13.7	2.9	78.9
Striped red mullet	<i>Mullus surmuletus</i> (L.)	37.4	2.4	7.3	52.9
Swordfish	<i>Xipbias gladius</i> (L.)	4.1	5.0	1.0	89.9
Thick blotched pickerel	<i>Spicara maena</i> (L.)	9.3	22.5	10.7	57.6
Thornback ray	<i>Raja clavata</i> (L.)	89.0	1.0	0.2	9.8
Tub fish	<i>Trigla lucerna</i> (L.)	75.1	4.1	2.1	18.6
White grouper	<i>Epinephelus aeneus</i> (Geoffroy Saint-Hilaire, 1817)	27.7	2.3	2.6	67.3
White sea bream	<i>Diplodus sargus</i> (L.)	9.6	6.9	5.5	78.0
Whiting	<i>Merlangius merlangus euxinus</i> (Nordmann)	66.5	6.2	0.6	26.8
Other fishes	(numerous spp.)	28.2	10.7	4.3	56.8
CEPHALOPODS					
Common squid	<i>Loligo vulgaris</i> (Lamarck, 1798)	45.0	3.9	30.5	20.7
Cuttlefish	<i>Sepia officinalis</i> (L.)	30.4	1.0	3.1	65.5
Flying squid	<i>Illex coindetii</i> (Verany, 1839)	94.1	0.7	1.9	3.3
Octopus	<i>Octopus vulgaris</i> (Cuvier, 1797)	48.6	1.6	6.8	43.0
Poulpes	<i>Eledone</i> spp.	97.9	0.3	0.8	1.1
CRUSTACEANS					
Crabs	Brachyura	30.5	0.0	0.8	68.7
Crayfish	<i>Nephtrops norvegicus</i>	92.9	0.6	1.5	4.9
Lobsters	<i>Homarus gammarus</i> (L.) and <i>Palinurus elephas</i> (Fabricius, 1787)	5.1	0.6	0.9	93.4
Common prawn	<i>Penaeus kerathurus</i> (Forsskål, 1775)	65.8	1.0	3.1	30.1
Shrimps	(no data on spp. composition)	69.8	0.4	0.5	29.3

Table 1 (continued).

The classification of the mean (1982-1989) commercial catch weight of all species for each subarea (Fig. 3) indicated that, at the 50% (Bray-Curtis) similarity level, the 16 subareas fall into three main groups: Group I (subareas 7 and 16 to 18), Group II (subareas 3 to 6, 8 to 10 and 15) and Group III (subareas 11 to 14), generally representing the southern Aegean and NW Levantine Seas, the Ionian and central Aegean Seas, and the N-NW Aegean Sea, respectively. The results of the ordination (MDS) of these subareas (Fig. 3) agree with the above pattern. The resulting stress value for the two-dimensional plot (Fig. 3) was low (=0.08), implying the adequacy of the MDS representation in these two dimensions.

The species compositions of the mean catches of the groups identified by multivariate analyses also differed considerably (Table 4). The mean catch of Group I was dominated by pickerel and bogue and, to a lesser extent, by horse mackerel, representing 21.0%, 17.6% and 8.5% of the mean total catch, respectively (Table 4). The mean catch of Group II was dominated by sardine, horse mackerel, bogue and pickerel, representing 12.1%, 12.0%, 11.3% and 10.2% of the mean

Species	Fishing subarea															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Anchovy	3	170	320	5	0	1101	96	876	265	2182	7901	4038	129	74	22	1
Bluefin tuna	1	0	7	0	0	47	0	106	0	115	418	733	33	2	245	5
Bluefish	0	1	0	4	0	5	0	8	0	2	71	102	5	1	2	2
Bogue	34	165	202	11	136	1104	48	673	13	442	522	610	1047	679	1356	542
Bonito	0	150	25	2	1	853	2	129	1	19	12	13	46	166	86	50
Chub mackerel	3	14	10	2	4	60	2	74	1	125	551	607	1020	434	129	6
European sardine	104	227	293	7	27	1369	129	650	56	646	3328	2860	716	12	111	37
Flying squid	1	1	19	0	0	51	9	36	1	8	57	41	32	1	6	19
Garnish	0	0	1	0	10	79	0	15	0	2	26	7	122	3	14	0
Gilt sardine	0	2	3	0	4	48	0	3	0	0	4	1	1	0	5	15
Horse mackerel	15	84	95	5	19	2008	57	752	12	356	1360	915	460	33	931	330
Jack mackerel	1	13	17	0	1	164	3	246	13	269	140	162	76	0	23	8
Mackerel	0	1	0	0	0	31	0	41	0	20	206	184	14	6	8	1
Skipjack	0	0	0	0	0	18	0	54	0	3	1	1	25	7	12	40
Sprat	1	5	10	0	0	10	2	7	0	0	2	0	14	1	0	0
Swordfish	21	96	69	0	14	115	5	9	0	40	5	10	20	272	138	251
Total pelagic	185	929	1072	36	218	7063	352	3679	361	4229	14606	10285	3759	1692	3087	1308
%	0.35	1.76	2.03	0.07	0.41	13.36	0.67	6.96	0.68	8.00	27.63	19.46	7.11	3.20	5.84	2.47
Anglerfish	1	1	1	0	0	23	0	63	1	1	328	54	25	0	3	2
Annular sea bream	1	0	9	2	0	11	1	28	2	9	169	44	7	2	1	1
Black sea bream	1	1	3	0	7	32	1	23	0	18	35	11	54	35	99	7
Blotched pickerel	68	19	80	0	0	7	5	111	2	30	97	71	34	1	1	8
Blue whiting	0	0	3	0	1	29	9	273	3	30	401	222	103	0	4	7
Bril	0	0	0	0	1	3	0	74	0	2	5	5	6	1	1	0
Comber	0	0	4	0	1	14	1	4	0	1	1	2	8	18	24	15
Common dentex	6	8	8	2	5	11	1	17	0	8	30	20	16	18	29	8
Common prawn	0	1	2	0	1	3	1	4	0	1	117	33	18	0	0	37
Common sea bream	2	1	4	0	5	22	1	7	0	12	14	11	72	23	47	67
Common squid	8	7	34	1	2	26	8	47	0	5	146	110	48	42	62	22
Crabs	0	0	0	0	0	2	0	14	0	0	17	4	0	0	0	0
Cuttlefish	6	3	33	2	1	15	4	40	1	7	484	280	57	4	12	38
Dogfish	3	1	15	0	3	2	2	0	0	1	4	22	77	0	1	62
Dusky grouper	2	4	9	0	2	5	1	1	0	1	4	4	5	6	2	50
European eel	0	0	0	1	0	2	0	0	0	1	6	2	0	0	0	1
European sea bass	1	0	3	2	0	3	1	49	0	2	71	9	1	2	2	1
Gilthead sea bream	5	5	4	0	0	3	1	124	0	34	23	20	1	17	1	0
Greater amberjack	1	0	1	1	2	17	2	6	0	2	4	2	3	3	4	3
Grey mullet	9	13	16	0	4	17	7	261	2	63	1366	400	29	4	7	1
Guitarfish	0	0	0	0	0	1	0	0	0	0	16	13	3	0	0	0
Gurnard	5	1	27	1	8	63	8	114	1	15	32	383	38	59	172	21
Hake	36	53	135	4	10	386	50	337	39	160	826	671	193	14	102	77

Table 2: Mean catch (in t) per species (or groups of species) and per fishing subarea, Greek waters, 1982-1989. Separation of species (or groups of species) into demersal/inshore and pelagic/semipelagic ones according to Stergiou and Pollard (in press).

Species	Fishing subarea															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
John dory	1	0	1	0	0	13	0	19	0	2	10	7	8	4	5	6
Large-eye dentex	0	14	8	1	1	21	2	6	0	2	3	7	28	3	7	5
Lobster	4	1	2	0	5	25	1	13	0	19	14	9	26	2	18	6
Norway lobster	0	0	0	0	0	47	9	69	1	22	453	274	66	1	11	1
Octopus	6	3	21	2	1	30	11	21	0	9	107	278	18	11	18	24
Other fish	39	61	69	5	109	389	65	338	14	155	3653	682	284	437	1219	218
Pickarel	99	270	427	26	450	994	80	491	7	177	197	241	557	844	1334	615
Octopi	3	2	12	0	0	27	2	20	0	4	326	141	15	2	11	26
Rays	3	2	10	0	0	26	1	22	0	9	5	16	17	1	3	1
Red mullet	37	39	65	0	35	197	10	213	4	81	468	344	104	77	49	71
Red pandora	19	7	23	4	14	110	6	169	2	46	16	35	44	53	106	24
Rockfish	1	1	11	1	0	2	1	37	0	3	7	6	1	1	0	1
Saddled bream	2	5	7	15	1	64	2	40	1	57	62	371	19	38	186	6
Salema	1	8	6	0	0	24	1	8	0	2	38	83	15	1	17	1
Scorpionfish	8	3	24	2	10	72	10	44	0	11	19	84	58	98	109	81
Shi drum	0	0	1	2	0	1	0	5	0	1	15	12	0	2	1	0
Shrimps	0	1	21	0	0	43	20	3	0	10	516	100	75	2	12	126
Smoothhound	3	1	20	2	3	18	5	6	0	31	65	140	42	2	6	16
Soles	4	2	9	0	2	22	2	62	0	12	540	489	7	9	5	5
Stone bass	1	8	15	0	10	9	0	13	0	7	3	7	44	3	10	90
Striped red mullet	20	15	58	2	70	208	9	225	2	72	140	196	128	179	405	169
Thick blotched pic.	3	10	13	0	8	90	1	46	2	41	66	36	68	33	53	9
Thornback ray	1	0	7	0	0	11	2	1	0	7	144	229	8	1	3	5
Tub fish	3	1	14	0	1	17	1	68	0	10	25	7	8	13	2	2
White grouper	1	3	6	1	4	11	1	1	0	5	1	1	2	2	2	23
White sea bream	6	8	8	1	6	37	1	24	1	22	36	49	27	26	124	23
Whiting	0	2	0	0	0	5	0	0	0	0	144	77	15	1	0	0
Total demersal	420	580	1251	80	788	3207	346	3564	87	1221	11266	6314	2485	2096	4292	1983
%	1.05	1.45	3.13	0.20	1.97	8.02	0.87	8.91	0.22	3.05	28.18	15.79	6.22	5.24	10.73	4.96

Table 2 (continued).

catch, respectively (Table 4). Finally, the mean catch of Group III was dominated by anchovy and sardine, representing 29.7% and 14.3% of the mean catch, respectively (Table 4).

The mean catch density (t/km^2) per group identified by multivariate analyses is shown in Table 5, together with mean catch density values from other ecosystems of the world ocean. It is evident that the mean catch density of pelagic, demersal and all fishes combined, increase from South to North. In addition, such an increase goes along with a decrease in the relative importance of demersal species. Hence, in Group I the mean catch density of the demersal species is higher than that of the pelagic ones whereas in Group III the former is about two times less than that of the pelagic ones (Table 5).

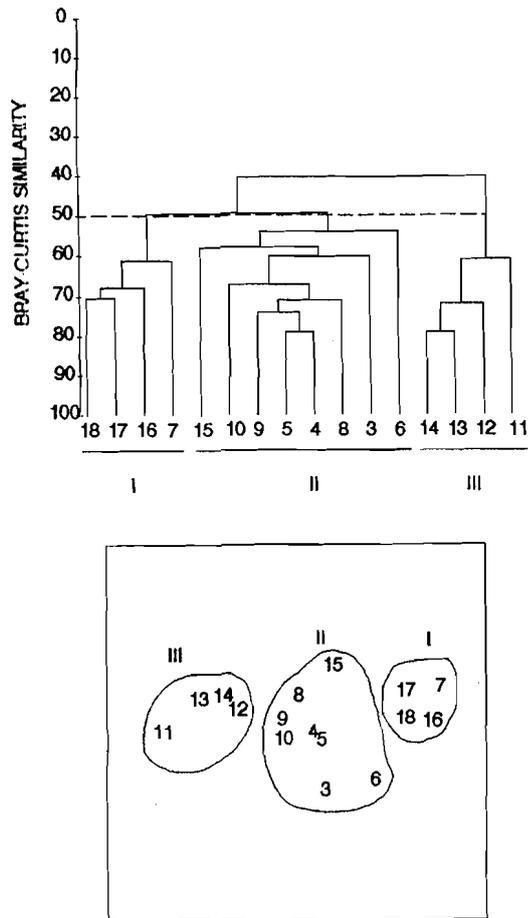


Fig. 3: Dendrogram (upper) for group-average clustering and MDS plot (lower), based on Bray-Curtis similarities between standardized mean catch weights, of all species from the 16 Greek fishing subareas, over the 1982-1989 period. For MDS plot orientation and scale are arbitrary.

3. DISCUSSION

Stergiou and Petrakis (1993) analysed the annual (standardized) commercial catch weights of the 66 species (or groups of species: Table 1) per component fishery for the years 1982-1987 (24 fisheries/year combinations). The classification and ordination of all species for each fishery/year combination indicated that the four fisheries fall into two main groups; Group A (trawlers, beach seiners and 'other coastal boats') and Group B (purse seiners), exploiting primarily demersal/inshore and primarily pelagic fisheries resources, respectively (Stergiou and Petrakis, 1993). Their results clearly reveal the multi-species and multi-gear nature of the Greek demersal/inshore and, to a lesser degree, pelagic/semi-pelagic fisheries. In addition, the results of the multivariate analyses (Fig. 3) suggested that the 16 Greek fishing subareas may be generally grouped into three geographical clusters that differ considerably from each other in terms of species composition (Table 4) and catch density (Table 5). Stergiou and Pollard (in press) did a similar analysis considering only

Fishing Subarea	C	N	D	H'	J
3	581	60	9.27	2.97	0.72
4	1480	62	8.36	2.70	0.65
5	2292	65	8.27	3.01	0.72
6	<u>96</u>	<u>56</u>	<u>12.05</u>	<u>3.38</u>	<u>0.84</u>
7	981	64	9.15	2.19	0.53
8	10237	<u>66</u>	7.04	2.77	0.66
9	667	64	9.68	2.90	0.69
10	7213	<u>66</u>	7.32	3.23	0.77
11	430	57	9.23	<u>1.67</u>	<u>0.41</u>
12	5422	<u>66</u>	7.56	2.43	0.58
13	<u>25842</u>	<u>66</u>	<u>6.39</u>	2.63	0.63
14	16568	<u>66</u>	6.69	2.91	0.69
15	6215	<u>66</u>	7.44	3.01	0.72
16	3757	<u>66</u>	7.89	2.59	0.62
17	7349	65	7.19	2.62	0.63
18	3260	64	7.79	2.93	0.71

Table 3: Mean total annual catch (C, in t), number of species (N), richness (D), Shannon-Wiener diversity (H') and evenness (J) per fishing subarea, Greek waters, 1982-1989. The highest and lowest values are underlined.

Species	Groups identified by multivariate analysis					
	Group I		Group II		Group III	
	Catch	%	Catch	%	Catch	%
Pickarel	<u>3243</u>	<u>21.0</u>	2945	10.1	—	—
Bogue	<u>2714</u>	<u>17.6</u>	3284	11.3	1586	3.2
Horse mackerel	1312	8.5	<u>3476</u>	<u>12.0</u>	2643	5.5
Striped red mullet	824	5.3	665	2.3	—	—
Swordfish	675	4.4	—	—	—	—
Chub mackerel	574	3.7	1186	4.1	1284	2.7
Bonito	303	2.0	1207	4.2	—	—
Scorpionfish	298	1.9	—	—	—	—
Gurnard	260	1.7	—	—	—	—
Bluefin tuna	253	1.6	—	—	1266	2.6
Sardine	—	—	<u>3495</u>	<u>12.1</u>	<u>6891</u>	<u>14.3</u>
Anchovy	—	—	2701	9.3	<u>14387</u>	<u>29.7</u>
Hake	—	—	1194	4.1	1696	3.5
Red mullet	—	—	664	2.3	897	1.9
Grey mullet	—	—	—	—	1831	3.8
Sole	—	—	—	—	1040	2.2
Others	5009	32.3	8190	28.2	14847	30.6

Table 4: Mean annual catches (in t) and percentages of the main species (or groups of species) per group identified by multivariate analysis (Fig. 3), Greek waters, 1982-1989. Catches and percentages for the two dominant species per group are underlined.

the ten Aegean Sea subareas for each year of the 1982-1987 period; they found that the within-subarea similarities were much more intense than the between-subarea ones (i.e., for each subarea and year of the 1982-1987 period subarea/year combinations were closely tied).

The main factors which may contribute to such a geographical differentiation most probably are the gradient in eutrophy, river runoff, temperature and salinity of the marine waters of Greece along a NNW to SSE axis. The eastern Mediterranean Sea is known to be one of the most oligotrophic marine regions of the world (Frigos, 1980, 1987; Azov, 1991). In the Aegean Sea, annual gross primary production in the outer part of subarea 8 and in the southern part of subarea 10 (see Fig. 1) was found to be 64 and 30 gC/m², respectively, the latter figure being among the lowest recorded for the Mediterranean Sea (Becacos-Kontos, 1968, 1977), comparable to those of the oligotrophic oceanic areas (50-70 gC/m²: Azov, 1991) and one to two orders of magnitude lower than those in the major upwelling areas (e.g., Peru, 1100 gC/m²: Chavez *et al.*, 1989; Cape Blanc and California, 730 and 150-720 gC/m², respectively: Mann and Lazier, 1991). Pavlova (1966), based on indirect estimations, suggested that secondary productivity in the Aegean Sea is 12 to 18 times lower than that in the Black Sea, four times lower than that in the Adriatic Sea, and similar to those of the Tyrrhenian and Libyan Seas. Data pertinent to secondary production in the Greek seas are only available for the Saronikos Gulf (Christou, 1991). Secondary production in the coastal area of the Saronikos Gulf (0.12-0.19 g/m³/yr) is low when compared with those recorded in other marine areas of the world (Table 6). Hence, the generally low secondary productivity of the Greek seas is evident, especially if one takes into account that Saronikos Gulf resembles, in terms of zooplankton density and species composition, many other gulfs of Greece, and its northern part is considered one of the most eutrophic areas of the country (Christou, 1991).

The oligotrophic nature of Greek waters is clearly depicted in the Coastal Zone Colour Scanner (CZCS) image of the phytoplankton-like pigment (PLP) distribution (not shown here, but see Stergiou and Georgopoulos, 1993), and reflected also to fisheries catch densities which, on the average, are lower than those of the Mediterranean Sea as a whole and in other areas of the world ocean (Table 5). However, within this generally oligotrophic environment relatively eutrophic areas do exist. Indeed, fishing subareas 8 and 10 to 14 are all characterized by one order of magnitude higher PLP concentrations as compared with the S-SE Aegean, NW Levantine and Ionian Seas (with the exception of subareas 5 and 9), the latter areas being comparable to the most oligotrophic open ocean areas of the world. A similar distribution pattern of PLP is also indicated for the wintertime, although concentrations, because of the winter mixing, are generally higher (N-NW rim of the Aegean Sea >0.5 mg/m³; Ionian, S-SE Aegean and NW Levantine Seas: about 0.2 mg/m³; Georgopoulos, unpubl. data). This general pattern of PLP distribution is also true of all the 46 images examined for the period 1981-1982 (Georgopoulos, unpubl. data), and coincides also with those of nutrient distributions in Greek waters, the latter being derived from historical data and from recent cruises in open sea (during 1986-1990) and coastal waters (during early 1980s) (Stergiou and Georgopoulos, 1993). Hence, the satellite image is representative of the general pattern of the spatial differentiation in PLP distribution in the Greek seas (Stergiou and Georgopoulos, 1993).

The spatial distributions of phytoplankton and zooplankton abundance in the surface waters as well as that of fisheries catch densities generally parallel that of PLP concentration. Hence, with respect to the offshore waters, phytoplankton abundance is higher in the N Aegean Sea, especially in the area bounded by 40° and 41°N latitude (subarea 14: 9 120-586 160 cell/l; Pagou and Gotsis-Skretas, 1989). Relatively high values (up to 72 090 cells/l) of phytoplankton abundance have been also recorded in the northern part of the Greek Ionian Sea (Pagou and Gotsis-Skretas, 1989). In contrast, the lowest values of phytoplankton abundance (<29 200 cell/l) have been recorded in the central and S-SE Aegean, central Ionian and NW Levantine Seas (Pagou and Gotsis-Skretas, 1989). With respect to zooplankton, its abundance is generally higher in some enclosed or semi-enclosed bays and gulfs (enclosed gulf in subarea 4, northern part of subarea 10, part of

subarea 8 close to Pireas Port, subarea 11: as high as 5 000 ind./m³) and in the offshore waters of the North Aegean Sea (from 500 to 5 000 ind./m³), especially in the area bounded between 40° and 41°N latitude (i.e., subareas 13 and 14), sometimes extending southward to 39.5°N (Siokou-Frangou and Pancucci-Papadopoulou, 1989; Siokou-Frangou *et al.*, 1991). The S-SE Aegean and NW Levantine Seas (southern part of subarea 16: Fig. 1) are oligotrophic areas comparable to open ocean ones, with zooplankton abundance usually ranging between 100 and 300 ind./m³ (Siokou-Frangou *et al.*, 1991). Moreover, zooplankton abundance attains relatively higher levels (up to 900 ind./m³: Siokou-Frangou *et al.*, 1991) in the northern part of the Greek side of the Ionian Sea (subarea 3: Fig. 1), when compared with the remaining part of the Ionian Sea (up to 500 ind./m³: Siokou-Frangou *et al.*, 1991).

In agreement with the above mentioned patterns, the mean (1982-1989) pelagic, demersal and total fisheries catch densities all decrease from 1.3, 0.83 and 2.13 t/km² in N-NW Aegean Sea to 0.25, 0.37 and 1.23 t/km² in S-SE Aegean Sea, respectively, with the latter density being comparable to those in the Ionian Sea (Table 5). The mean pelagic catch density in the Ionian and S-SE Aegean Seas is from 3 to 150 times lower than those in other marine areas of the world ocean (Table 5). In contrast, the mean pelagic catch density in the N-NW Aegean Sea (Group III) is: (a) comparable to that in the California coast (22-38°N), (b) higher than those in the Gulf of California and Indian waters (7-25°N), and (c) 2 to 30 times

Geographic area	Catch (t)		Area in (km ²)	Density (t/km ²)		
	Pelagic*	Demersal*		Pelagic	Demersal	Total
Greek seas (total)	52861	39979	75294	0.70	0.53	1.23
Group I	6304	9159	24998	0.25	0.37	0.62
Group II	17076	11932	27613	0.62	0.43	1.05
Group III	29481	18888	22683	1.30	0.83	2.13
Ionian Sea	2574	2677	9824	0.26	0.27	0.53
Aegean Sea	50287	37303	65470	0.77	0.57	1.34
N-NW Aegean Sea	29120	18801	22010	1.32	0.85	2.18
S-SE Aegean Sea	21166	18502	43460	0.49	0.43	0.91
Mediterranean	—	—	—	1.40	—	—
West Africa (6-36N)	—	—	—	3.14	—	—
Côte-d'Ivoire (8W-1E)	—	—	—	2.17	—	—
South Africa (6-37N)	—	—	—	3.75	—	—
California (22-38N)	—	—	—	1.75	—	—
Gulf of California (24N)	—	—	—	0.87	—	—
South America (1-43N)	—	—	—	38.40	—	—
India (7-25N)	—	—	—	0.97	—	—
Spain (36-44N)	—	—	—	3.35	—	—
North Sea	—	—	—	—	—	4.70
Cape Hateras to Nova Scotia	—	—	—	—	—	1.54
Eastern Bering Sea	—	—	—	—	—	2.10
Central Baltic Sea	—	—	—	—	—	2.75

*Separation of the 66 species (or groups of species) into pelagic/semipelagic and demersal/inshore according to Stergiou and Pollard (1994).

Table 5: Catches and densities of pelagic and demersal fishes in Greek waters and other ecosystems of the world ocean. Data for Mediterranean from Ben-Tuvia (1983), West Africa to Spain from Cury (1995), and for North Sea to Central Baltic Sea from Sparholt (1990).

lower than those in the major upwelling areas of the world (Table 5). The mean total catch density in S-SE Aegean Sea is from 2 to 7 times lower than those in the remaining areas of Greece, the Mediterranean as a whole and other areas of the world ocean (Table 5). In contrast, the mean total catch density in N-NW Aegean Sea is comparable to that in the E Bering Sea and two times higher than that of the Mediterranean as a whole (Table 5).

It must also be stressed that in the SE Mediterranean Sea the importance of picoplankton is high, a fact which presumably increases the number of trophic levels and, hence, may limit the potential production at higher trophic levels (Azov, 1991), possibly resulting in a lower biomass of small- and medium-sized pelagic fishes. This is consistent with the north-to-south decline in the mean pelagic catch density (Table 5) and with the results of echo-surveys undertaken during May 1989 - May 1992 in fishing subareas 12 to 15. The echo-surveys revealed that the echo-abundance (mm deflection per km²) of small- and medium-sized pelagic fishes in fishing subareas 13 and 14 are higher by an order of magnitude than those in fishing subareas 12 and 15 (Stergiou *et al.*, 1993; Papaconstantinou *et al.*, 1994).

It is worthy to point out also that in the summertime (mainly from July to September) upwelling, driven by the Etesian winds (dry and cool N-NE-E winds blowing over the Aegean Sea) which very often reach gale force, takes place along the eastern Aegean coast (e.g., Metaxas, 1973). In contrast to other areas where seasonal upwelling takes place (e.g., Ivorian and Ghanaian coasts: Koranteng and Pezennec, this vol.; Venezuelan coast: Mendoza *et al.*, this vol.) seasonal upwelling along the E Aegean coast probably has no significant impact on the primary production of the area (Georgopoulos, pers. comm.) as well as on fisheries catch densities (Table 5). This could be attributed to the fact that upwelled waters reach the surface from layers immediately below the seasonal thermocline, its depth in the E Aegean Sea generally being <50 m, and, hence, are already poor in nutrients (Georgopoulos, pers. comm.). However, this issue calls for thorough studies.

Subareas 8, 12, 13 and 14 are under the influence of natural eutrophication processes. Hence the above mentioned subareas are all directly influenced by nutrient inputs from outflowing Black Sea waters. These waters enter the Aegean Sea from the Dardanelles Strait and are colder, less saline and much richer in nutrients than the waters of Levantine origin that enter the Aegean Sea mainly from the eastern straits of the Cretan Arc (Theocharis and Georgopoulos, 1992; Georgopoulos *et al.*, 1989). Freshwater runoff is also relatively important along the northern rim of the Aegean (17,657 x 10⁶ m³/yr) as compared to the remaining part of the Greek side of the Aegean Sea (<1,000 m³/yr; Therianos, 1974). Other factors which contribute to the relative high eutrophy of subareas 8 and 10 to 14 may include: (a) the extended continental shelf of subareas 8, 13 and 14 (Fig. 1); (c) localized anthropogenic eutrophication (see Fig. 1; Friligos, 1980, 1987); and (d) upwelling in the northern part of subarea 10 (Balopoulos and Papageorgiou, 1991). The high values of phytoplankton pigment concentration (about 1 mg/m³) along the northern coast of the Aegean Sea may be partly attributed to suspended material derived from river runoff.

In the Ionian Sea, catch densities (Table 5) and PLP concentrations are much higher in subareas 5 and 9. This must be attributed to the systematic wind-driven upwelling along the northern coast of these subareas (Laskaratos *et al.*, 1989), although river runoff (6,861 x 10⁶ m³/yr; Therianos, 1974) is also important in subarea 5.

The salinity and temperature differences in Greek waters may also be related to the geographical grouping of the 16 fishing subareas. Hence, the lower salinity prevailing along the coasts of subareas 13 and 14, which are influenced by the Black Sea waters and river runoff, may explain the predominance of the relatively euryhaline grey mullet and sole in the N-NW Aegean Sea (Group III: Table 4). In addition, the pelagic anchovy, sardine and horse mackerel and the demersal hake, which dominate the pelagic and demersal catches, respectively, are replaced by bogue and pickerel, respectively, in the S-SE Aegean and NW Levantine Seas (Group I: Table 4). Both bogue and pickerel are generally characterized by a more southern distribution (they are not found to the north of Portugal in Atlantic waters) as compared to anchovy, horse mackerel and

hake (Whitehead *et al.*, 1984). It is worthy to note that the species dominating the pelagic and demersal catches (i.e., anchovy, sardine, horse mackerel hake: Table 4) of the colder, less saline and relatively more eutrophic N-NW Aegean (Group III) are known to inhabit the major upwelling areas of the world. Also, Stergiou (1992a) has suggested that seasonal upwelling, driven by the Etesian winds, may also take place along the N-NE coast of the Aegean Sea, a fact that may also explain, in a synergetic fashion with the presence of Black Sea waters, the relatively high productivity of the waters in subarea 14. However, such a wind-driven upwelling has not so far been justified from field studies.

The management implications of these results have been discussed elsewhere (Stergiou, 1992b; 1993; Stergiou and Petrakis, 1993; Stergiou and Pollard, in press; Stergiou *et al.*, 1994) and are briefly summarized below. Catch-effort studies as well as experimental trawl and echo-surveys all suggest that Greek demersal/inshore and pelagic fisheries resources are overfished (Stergiou *et al.*, 1994). Hence, the need for rational management of the Greek demersal/inshore and pelagic fisheries resources is urgent. The inadequacy of the national management regulations currently in force for the demersal and inshore fisheries has been discussed by Stergiou *et al.* (1992); despite the reinforcement of these measures, demersal and inshore fisheries resources are currently overfished (Stergiou *et al.*, 1994). The same must be true of pelagic resources. Such an inadequacy must be mainly attributed to the multi-species, multi-gear nature of the Greek and, in general, of the Mediterranean fisheries that poses certain difficulties in designing and implementing uniform protective measures, particularly so for the demersal/inshore fisheries. Recent evidence (see reviews by Davis (1989), Bohnsack (1990), Roberts and Polunin (1991) and Pollard (1993)) indicates that one of the most potentially effective management techniques to enhance the spawning success of inshore demersal and reef fishes, and particularly those contributing to multi-species fisheries, would be by the creation of marine harvest refugia that provide a refuge in space rather than a refuge in numbers, the latter being the aim of most traditional fisheries management measures. Such a measure as the creation of marine harvest refugia is potentially applicable in the case of the Greek fisheries.

Area	Period	Daily production	Annual production	Group	Reference
Baltic Sea	Y	—	1.5-4 gC m ⁻²	Z	Wulff <i>et al.</i> (1977)
Pacific Ocean (Japan)	—	10-60 mgC m ⁻²	—	Z	Ikeda and Moroda (1978)
Osaka Bay (Japan)	—	0.8-85 mgC m ⁻³	—	Z	Joh and Uno (1983)
West Coast of Sweden	Y	—	1-2 gC m ⁻²	Z	Baamsteadt (1984)
North Atlantic Ocean	Y	—	7 mg m ⁻²	Z	Razouls (1985)
St. Lawrence Gulf (Canada)	—	29 mgC m ⁻²	—	Z	Citarella (1985)
Indian Ocean	—	15-47.8 mgC m ⁻²	—	Z	Goswami (1985)
Baltic Sea	Y	—	3.1-7.8 gC m ⁻²	Z	Kankaala (1987)
Westernport Bay (Australia)	Y	—	1 gC m ⁻²	Z	Kimmerer and McKinnon (1987)
Eastern Mediterranean	Y	0.05-3.9 mg m ⁻³ (0.32-18.86 mgC m ⁻²)	0.12-0.19 g m ⁻³ (0.58-0.93 gC m ⁻²)	Z	Christou (1991)
Scotian Shelf (Canada)	Y	—	21.6 g m ⁻²	C	Tremblay and Roff (1983)
North Sea	May-Oct	—	9 g m ⁻²	C	Fransz <i>et al.</i> (1984)
Inland Sea (Japan)	Y	—	33.7 gC m ⁻²	C	Uye <i>et al.</i> (1986)
Skagerrak	Aug	3-8 mgC m ⁻³	—	C	Peterson <i>et al.</i> (1991)

Table 6: Zooplankton production in different areas of the world ocean. Y=entire year; —=no data available; dominant group: Z=zooplankton. C=copepods.

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