The influence of caged mariculture on the early development of sublittoral fouling communities: a pan-European study

E. J. Cook, K. D. Black, M. D. J. Sayer, C. J. Cromey, D. L. Angel, E. Spanier, A. Tsemel, T. Katz, N. Eden, I. Karakassis, M. Tsapakis, E. T. Apostolaki, and A. Malej

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The development of fouling communities was assessed to investigate the influence of caged mariculture on sublittoral epibiota. Artificial structures were deployed within 10 m of caged mariculture and at a "reference" location between 150 and 500 m of the study site at four coastal locations (Oban, Scotland; Sitia, Crete; Piran, Slovenia; and Eilat, Israel). The fouling community on the artificial structures was measured both quantitatively and qualitatively bi-monthly between June 2001 and December 2001. Multivariate statistical analysis was used to compare community structure between the study sites and locations. Artificial structures deployed at the mariculture site supported a higher epibiotic biomass than at the reference site at Oban and Eilat. Community composition was significantly different between the mariculture and reference site at Eilat. The biological succession on the structures changed from an autotrophic to a heterotrophic mode over the experimental period at all locations with the exception of Oban, where negligible quantities of macroalgae were observed on the structures. Differences in community biomass and succession observed between artificial structures deployed at mariculture and reference sites, particularly in oligotrophic environments, may be caused by enhanced larval settlement and an elevated supply of particulate material and dissolved nutrients to structures adjacent to the fish cages.

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E. J. Cook, K. D. Black, M. D. J. Sayer, and C. J. Cromey: Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban PA37 1QA, Scotland, UK. D. L. Angel, E. Spanier, and A. Tsemel: The Leon Recanati Institute for Maritime Studies and Department for Maritime Civilizations, University of Haifa, Haifa 31905, Israel. T. Katz and N. Eden: The Inter-University Institute of Eilat, PO Box 469, Eilat 88103, Israel. I. Karakassis: Biology Department, University of Crete, Iraklion 71409, Greece. M. Tsapakis and E. T. Apostolaki: Hellenic Centre for Marine Research, PO Box 2214, Iraklion 71003, Greece. A. Malej: Marine Biological Station Piran, National Institute of Biology, 6330 Piran, Slovenia. Correspondence to E. J. Cook: tel: +44 1631 559000; fax: +44 1631 559001; e-mail: ejc@sams.ac.uk.

Introduction

Food availability and quality play an important role in the length of settlement competence in larval marine invertebrates (Kelly, 2002), the nature of the existing biota on the substrata (Anderson and Underwood, 1994), and the subsequent growth and succession of marine organisms that successfully recruit to a particular location (Ambariyanto and HoeghGuldberg, 1997; Fleury *et al.*, 2000). Bombace (1989) observed that eutrophic waters produce very different communities than oligotrophic waters. For

example, the abundance and production rates of filterfeeders such as mussels and oysters have been described on the artificial reefs in the eutrophic waters of the Adriatic Sea (Badalamenti *et al.*, 1992).

Caged fish culture releases dissolved inorganic nutrients and particulates, such as uneaten fish feed and faecal material, directly into the water column. These components are released in a highly biologically active form, and the effect of the particulate material on soft-bottom, benthic communities has already been documented (Brown *et al.*, 1987; Weston, 1990; Findlay *et al.*, 1995; Karakassis *et al.*,

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2000; Ruiz et al., 2001; Vezzulli et al., 2002; La Rosa et al., 2004; Piazzi et al., 2004). These effects typically follow a specific pattern, characterized by an initial increase in community diversity as the food supply is enhanced, followed by a rapid decline in species number, as the surface sediments become habitable to just a few specialized species (Pearson and Rosenberg, 1978). The distance and hydrodynamic conditions from the site of caged mariculture activity typically determine the diversity of the benthic community in a particular location (Karakassis et al., 2000). Studies on the effects of point-source anthropogenic pollution on hard-substrata encrusting macrobenthic assemblages have found that the composition of these communities can be significantly altered by exposure to sewage pollution (Roberts, 1996; Roberts et al., 1998). However, the influence of elevated nutrient availability on hardsubstrata communities associated with caged fish culture has received little attention. Studies have shown that diverse, hard-substrata epibenthic communities will colonize artificial structures adjacent to caged mariculture (Angel and Spanier, 1999; Angel et al., 2002) and assimilate fishfarm-derived particulate material (Lojen et al., 2003). High levels of dissolved organic carbon (La Rosa et al., 2002), phosphate, and ammonium (Pitta et al., 1998) have also been found in waters adjacent to fish farms in the Mediterranean Sea. However, there is a general paucity of information on the effects of dissolved nutrients released by mariculture on the immediate environment (Pearson and Black, 2001).

Epibenthic communities are composed, in general, of suspension feeders and macroalgae, depending on the depth and location of the substrata. The communities extract dissolved and particulate matter from the water column with varying degrees of efficiency (see review Hughes et al., 2005), and it has been suggested that they could be used to mitigate the environmental impact of open-water aquaculture (Apostolaki et al., 2003; Cook and Black, 2003; Spanier et al., 2003). Bivalves in particular have attracted attention as potential biofiltration organisms, and a significant control of eutrophication by bivalves was recorded in a Chilean lake by Soto and Mena (1999). In closed tank systems containing salmon (Salmo salar), freshwater mussels (Diplodon chilensis) reduced concentrations of chlorophyll a by two orders of magnitude in 18 days, converting a hyper-eutrophic to an oligotrophic situation. Further evidence supporting the mitigating potential of mussels was reported by Newell and Richardson (2000), who used a computer simulation to model the complex patterns of water flow around mussels suspended on lines. Depletion of seston by up to 50% was indicated by the model and later recorded in field trials.

The enhanced growth of mussels (Stirling and Okumus, 1995; Cook and Black, 2003) and macroalgae (Troell et al., 1997; Chopin et al., 1999; Chung et al., 2002) has been attributed to the nutrient enrichment of the water column adjacent to caged mariculture. Studies utilizing

macroalgae to remove dissolved metabolic products, have estimated the removal of >90% of the dissolved inorganic nitrogen released by land-based fish cultivation (Cohen and Neori, 1991; Buschmann *et al.*, 1994). In open-cage cultivation, elevated growth rates and nitrogen assimilation have been found in macroalgae cultivated in the vicinity of the fish cages (Troell *et al.*, 1997; Chopin *et al.*, 1999).

The present study examines epibenthic community development in association with mariculture developments over a range of experimental conditions. The study compares the early development of hard-substrata benthic communities on artificial substrata adjacent to commercial mariculture activity with those deployed at reference sites. Artificial structures may not represent the exact nature and complexity of natural habitats, but they are be an effective means of studying the short-term processes of recruitment (Rodriguez *et al.*, 1993; Glassom *et al.*, 2004). The term recruitment is used in the present context to refer to the processes leading to settlement and metamorphosis of larvae and their survival until observation (Rodriguez *et al.*, 1993; Holmes *et al.*, 1997).

Material and methods

Four study sites (Figure 1) were chosen to represent overlapping temperate and subtropical environments from NW Europe (Scotland, Oban), through to the Mediterranean (Slovenia, Piran and Crete, Sitia) to the northern Red Sea (Israel, Eilat). At each site, identical artificial substrata were deployed at a distance of either 3–10 m (hereafter known as "Fish farm" or FF) or 150–500 m (hereafter known as "Reference site" or R) from the mariculture

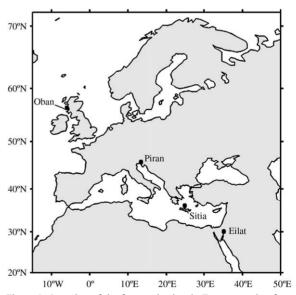


Figure 1. Location of the four study sites in Europe ranging from northwestern Europe to the Gulf of Aqaba, Red Sea.

activity. The substrata consisted of black NETLONTM (Str 7011) square mesh (25 mm), formed into cylinders (500 mm height; 250 mm diameter, and total surface area for attachment of 0.48 m²) and mounted on plastic rectangular frames constructed from 1.3 and 0.7 cm ABS piping and fittings. Each frame held eight mesh cylinders at a distance of 0.25 m apart. Four frames were deployed at the fish farm and reference site, a total of 32 cylinders at each site. This gave a total of four replicate mesh cylinders at the FF and R for each sampling event. Five mesh cylinders remained on each frame at each site in case of loss or damage. The anchor moorings and sets of buoys used to facilitate removal and replacement of the mesh cylinders were slightly different in design at each study site because of variations in bottom depth, current velocity, and local navigation requirements. However, the mooring design enabled the mesh cylinders to be held at a depth of approximately 8 m from the surface; differences in the mooring system were not expected to influence the performance of the artificial substrata. The frames at each study site were held vertically in the water column and orientated perpendicular to the predominant current direction in order to maximize their exposure to suspended particles. The artificial structures were deployed at the four sites between 18 and 29 June, and 22 December 2001. Environmental variables including temperature and salinity were measured monthly throughout the 6-month experimental period. Unfortunately, technical difficulties prevented the first sampling of the artificial structures in Eilat, and fishing activity in Sitia led to the abandonment of the experiment and its repeat in 2002, with filters placed solely at the fish farm site. In addition, logistical problems with sampling the structures simultaneously at all study sites meant that data are presented within 2-month time intervals.

Study sites

United Kingdom

The Firth of Lorne, Oban, on the west coast of Scotland (hereafter referred to as Oban) is a large sealoch, stretching from the narrow (180 m) mouth of Loch Linnhe in the north to the wide (25 km) opening to the Atlantic in the south (Pearson, 1970). The firth is approximately 60 km long and an average of 8 km wide. The total annual freshwater run-off into the loch system is 80×10^7 m³, although the influence of the run-off is typically confined to surface waters (Barnes and Goodley, 1958). The water column undergoes vertical mixing in winter (January-April; Pearson, 1970), which elevates surface nutrient levels and leads to increased concentrations of surface chlorophyll α , with an annual peak in May (Grantham, 1981). The study site was located in the middle of the firth, on the eastern side of the sealoch approximately 500 m from shore, in a depth of 30-45 m. It was moderately tidal, and surface mean and maximum current speeds of 4.6 and 21.0 cm s⁻¹, respectively, were measured over a 29-day period (CJC, unpublished data). The residual current direction is northeast, and the residual speed was particularly strong at mid-depth (4.4 cm s⁻¹) and near-bed (2.9 cm s⁻¹). During weaker neap tides, wind forcing caused variation in residual direction. The artificial structures were deployed 10 m northeast of the fish farm and at a reference site 500 m east of the farm.

Slovenia

The Bay of Piran, on the north coast of the Adriatic Sea (hereafter referred to as Piran) is a semi-enclosed bay connected to the surrounding marine area by a narrow (5.5 km) opening at the northwestern part of the bay. The bay is about 7 km long and 5 km wide, and its inner part ends with highly saline saltpans (about 650 ha) created by the River Dragonja, whose mouth is about 1.5 km from the fish farm. The river is typically torrential (average yearly outflow about $3.7 \times 10^7 \,\mathrm{m}^3$), although it virtually dries out during summer. The region typically experiences mean and maximum current speeds of 5.1 (depth 4 m) and 15.8 cm s⁻¹, respectively. The residual current direction is northeast, and the residual speed is relatively strong at mid-depth (3.6 cm s^{-1}) and near-bottom (3.7 cm s^{-1}) ; Malačič and Forte, 2003). The study site was located in the inner part of the bay in a water depth of 12-14 m. The artificial structures were deployed 3 m east of the fish farm and at a reference site 150-200 m north of the farm.

Crete

Sitia Bay (hereafter referred to as Sitia) is on the northeast coast of Crete in a fairly open coastal bay facing the southern Aegean Sea, with little anthropogenic activity within 10 km of the bay. It is relatively sheltered by a rocky slope to the east. The marine environment in the surrounding area is typical of the oligotrophic conditions of the eastern Mediterranean, with high transparency in the water column and low chlorophyll and nutrient concentrations. Surface mean and maximum current speeds of 4.1 and 10.1 cm s⁻¹, respectively, were measured over a period of 34 days. Near-bottom maximum speeds were similar to those at the surface, but in general were much more quiescent, reflected by the mean of 1.8 cm s⁻¹. The study site was approximately 300 m from shore and depths ranged from 12 m landward to a maximum of 30 m seaward; the average depth below the fish farm was 15-20 m. The environment was highly affected by wind-generated surface currents, but with the complex topography at the site, residual current was weak and the direction unpredictable. The artificial structures were deployed 10 m northwest of the fish farm and at a reference site 500 m west of the farm.

Israel

Eilat is located at the northern tip of the Gulf of Aqaba, a semi-enclosed sea surrounded by deserts (annual rainfall generally does not exceed 10 mm) and connected to the

Red Sea by a narrow opening (Straits of Tiran) at the southernmost part. The Gulf is oligotrophic, but it undergoes an annual deep vertical mixing event during winter/spring (Genin et al., 1995) that elevates surface nutrient levels and leads to a spring algal bloom (Reiss and Hottinger, 1984; Lindell and Post, 1995). The study site is in the northern part of the Gulf of Agaba, situated adjacent to the Israel-Jordan border and located approximately 300 m from shore in a depth of 20-35 m. Large cylindrical fish farm cages were moored along a northeast-southwest axis, perpendicular to the dominant currents in this part of the Gulf. The area typically experiences surface mean and maximum current speeds of 5.0 and 31.0 cm s⁻¹, respectively. The residual current direction was northeast, and the residual speed was relatively weak at the surface (1.6 cm s^{-1}) and near-bottom (1.0 cm s^{-1}) ; Cook et al., 2004). The artificial structures were deployed 10 m west of the fish farm and at a reference site 300 m west of the farm.

Methodology

The fish farms in Piran, Sitia, and Eilat raise gilthead sea bream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*), whereas the farm in Oban raises Atlantic salmon. Fish biomass was greatest in Crete, with a maximum of 1000 t, and lowest in Piran (50 t) during the experimental period. The maximum biomass of Atlantic salmon recorded at Oban was 890 t, and at Eilat, the biomass of *S. aurata* and *D. labrax* reached 620 t.

The artificial structures were sampled bi-monthly over a 6-month period of exposure, four replicate structures being selected randomly from the fish farm and reference site at each study site. The mesh cylinders were removed from their frames *in situ* using scuba, and new mesh cylinders were attached in their place as a means of maintaining the general hydrodynamic environment surrounding the frame. Mechanical disruption and loss of biota from the cylinders during the removal and transportation process to the laboratory were minimized.

The epibiota were assessed by unaided inspection or by using a low-power dissection microscope. Organisms were identified to the lowest possible taxonomic level. Distinct colonies of each colonial species were counted as one individual colony. Motile organisms were noted as present or absent. The edges of overlap on the cylinders were not assessed. After taxonomic assessment, the biomass of each dominant group was calculated by removing the organisms from the cylinders and drying the samples at 45°C until a constant dry weight was obtained.

The treatment (two levels) and sampling time (three levels) were used as fixed factors in a two-way ANOVA to test for differences in biomass of the fouling communities between the treatments at Oban, Piran, and Eilat (MINITAB, Release 13.32 for Windows). One-way ANOVA was used to test for differences in biomass for each

treatment between the study sites at the end of the experimental period. Bartlett's test was used to test for homogeneity of variances (Zar, 1996), and Tukey's multiple comparison test was used in pairwise comparisons to assess significant differences between areas.

Community structure was assessed between each site, treatment, and exposure period by non-parametric multivariate techniques on transformed data (square root) using the software package PRIMER (Clarke and Warwick, 1994). A triangular similarity matrix was constructed using the non-metric Multi-Dimensional Scaling (nMDS) program, selecting the Bray—Curtis similarity measure. Two-way analysis of similarity (ANOSIM) tests were performed to examine the differences in epifaunal assemblage composition between each treatment and sampling event for Oban, Piran, and Eilat. The similarity percentages procedure (SIMPER) within the PRIMER software was used to identify the major species contributing to the dissimilarity measure obtained (Clarke and Warwick, 1994).

Results

Environmental data

The study sites at Piran and Sitia showed the largest change in seawater temperature over the 6-month study period, with declines of 8.9°C and 9.0°C, respectively. At Oban and Eilat, the change in temperature was similar between the two sites, with decreases of 3.3°C and 3.8°C, respectively. The lowest seawater temperature was at Oban and the highest at Eilat (Table 1). Fluctuations in salinity were greatest at Piran, where the salinity changed by 1.7 psu over the study period, while the study sites at Oban, Sitia, and Eilat experienced only minor changes in salinity (\leq 0.6 psu; Table 1).

Community biomass

The total cumulative biomass of epibiota on the artificial structures increased at the mariculture and reference locations at all the four sites (Figure 2). There was a significant difference in biomass between the fish farm sites and the references sites at Oban, Eilat, and Piran (Table 2). At Oban and Eilat, the artificial structures deployed close to the fish farms supported a greater biomass of epibiota than the reference sites over the experimental period (Figure 2). Conversely, the biomass at the reference site (R)

Table 1. Physical characteristics of study sites, showing maximum and minimum temperature and salinity for the experimental period.

Parameter	Oban	Piran	Sitia*	Eilat
Temperature (°C) Salinity (psu)			16.0-25.0 39.0-39.6	

^{*}Data are for June-December 2002.

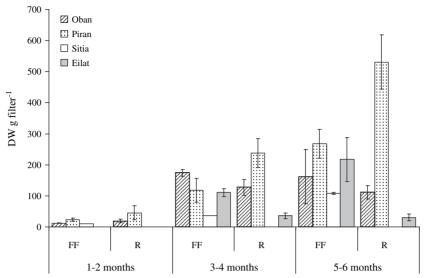


Figure 2. Total biomass at the four study sites after exposure periods of 1-2, 3-4, and 5-6 months after deployment. Mean dry weight (DW, g) per mesh filter (\pm s.d.) is shown for the fish farm (FF) and reference site (R) at each location.

was greater than at the fish farm at Piran (Figure 2). The greatest difference in biomass between the treatments was at Eilat, where the artificial structures deployed adjacent to the fish farm (FF) supported seven times the biomass of fouling epibiota compared with the structures at the reference site after 5–6 months of deployment (Table 2). The epibiotic biomass after 5–6 months on structures adjacent to the FF sites was significantly higher at Piran than at Oban or Crete (one-way ANOVA; F = 4.38, p < 0.05), but it was not significantly different from that at Eilat. At the R sites, Piran had a greater biomass on the artificial structures than Oban and Eilat, particularly after 5–6 months (one-way ANOVA; F = 79.74, p = 0.001; Figure 2).

Community composition

The total number of species in the fouling communities that colonized the artificial structures during the 6-month study period varied between sites. At Piran and Eilat the species number was similar, at 30 and 26 species, respectively. At Oban, 40 species were recorded, and at Sitia there were 73 species (Table 3). Difficulties in resolving certain groups to species level may mean that the values for Piran and Eilat underestimate the total number of species there. At Eilat the species number (mean \pm s.e.) was greater on the structures deployed at the FF (12 \pm 0.5 species) than at the R site (9 \pm 0.4 species), whereas Piran had more species at the R site (13 \pm 3.9 species) than at the FF site (10.5 \pm 1.5 species) after 5–6 months. There was no difference in species number between the FF (21.5 \pm 2.4 species) and the R site (22.3 \pm 1.7 species) at Oban.

Community composition on the artificial structures between the FF and R sites at each of the sampling times shows clear within-site trends in most cases (Figure 3).

The clustering and spatial overlap of treatment levels varied considerably between sampling event and study site, indicating differences in the rate of change in community composition over the experimental period, and in community structure between the FF and the R sites. ANOSIM showed a significant difference (p < 0.05) in community structure between the FF and R sites at Piran and Eilat at each sampling event (Table 4). No significant difference was found between the community assemblages on the artificial structures between the FF and R sites after 1-2 and 5-6 months of deployment at Oban (p > 0.05, Table 4).

Table 2. Two-way analysis of variance for biomass of epibiota on artificial structures deployed at fish farm and reference sites at Oban, Piran, and Eilat (n = 4).

Source	d.f.	Mean square	F	<i>p</i> -value
Oban				
Treatment (T)	1	0.076	15.68	p < 0.001
Time	2	2.55	523.65	p < 0.001
$T \times time$	2	0.001	0.26	NS
Residual	18			
Piran				
Treatment (T)	1	0.523	30.79	p < 0.001
Time	2	2.431	143.23	p < 0.001
$T \times time$	2	0.001	0.08	NS
Residual	18			
Eilat				
Treatment (T)	1	1.86776	72.67	p < 0.001
Time	1	0.03206	1.25	NS
$T \times time$	1	0.12695	4.94	NS
Residual	12			

Table 3. List of species identified at the four study sites over the experimental period.

Phylum	Oban	Piran	Sitia	Eilat
Chlorophyta		Cladophora sp. Enteromorpha sp.	Chlorophyta	
Rhodophyta	Rhodophyceae	Antithamnion sp. Ceramium sp.	Rhodophyta	Jania sp.
		Champia sp. Polysiphonia sp.		Lithothamnion sp.
			Phaeophyta	
Porifera			Demospongiae Hyalospongiae	Mycale fistulifera Beige rough sponge Beige encrusting sponge Violet encrusting spong
Cnidaria	Obelia longissima Tubularia larynx	Campanopsis sp. Kirchenpaueria sp. Obelia sp.	Cerianthus sp. Octocorallia	Aiptasia pulchella Boloceroides mcmurrichi Zebra hydrozoa Thyroscyphus fruticosus Yellow hydrozoa
Nemertea Nematoda Sipuncula	Emplectonema neesi	Nematoda	Nematoda Aspidosiphon muelleri Golfingia sp. Phascolion strombus	
Annelida	Aphrodita sp. Eunicidae Nereis sp. Platynereis dumerilii Sabella pavonina Spirobis sp. Syllidae Terebellidae	Ceratonereis costae Ceratonereis hircinicola Lysidice ninetta Nereis lamellosa Pomatoceros sp. Spirorbis sp.	Alciopidae Arabella iricolor Autolytus sp. Brachiomma sp. Chone duneri Chrysopetalum debile Ctenodrilus serratus Dorvillea rubrovittata Eulalia sp. Exogone verrugera Harmothoe sp. Lysidice ninetta Pseudomystides limbata Nematonereis unicornis Odontosyllis sp. Pectinaria sp. Pista cristata Platynereis dumerilii Polyophthalmus pictus Protodorvillea kefersteini Serpula sp. Spirobranchus polytrema Syllis hyalina Syllis sp.	Hydroides exaltatus Hydroides minax Hydroides perezi Josephella marenzelleri Salmacina sp. Serpula sp.
Crustacea	Aora gracilis Balanus balanus Cancer pagurus Caprella mutica Gammaridae Idotea sp. Jassa falcata Macropodia sp.	Balanus balanus Corophium sextonae Gammaridae Ischyrocerus inexpectatus Pseudoprotella phasma	Alpheus dentipes Amphithoe ramondi Athanas nitescens Caprella acantifera Phtisica marina Copepoda Dexamine spinosa Dromia personata	

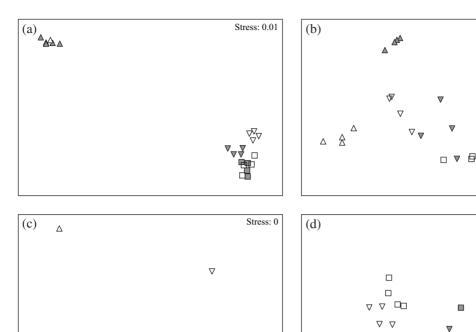
Table 3. (continued)

Phylum	Oban	Piran	Sitia	Eilat
	Mysidae Pinnotheres pisum		Elasmopus pocillimanus Ericthonius punctatus Galathea sp. Jassa marmorata Leptochelia savignyi Mysidacea Pilumnus hirtellus Pilumnus sp. Processa acutirostris Processa sp. Pycnogonida Sphaerosomatidae Stenothoe gallensis Synalpheus sp. Tanais dulongii Thoralus cranchii	
Mollusca	Abra alba Aequipecten opercularis Ancula gibbosa Anomia ephippium Flabellina pedata Hiatella artica Modiolarca tumida Mytilus edulis Pecten maximus Rissoidae	Arcidae Cardiidae <i>Ostrea</i> sp. Nudibranchia	Arca noae Bittium reticulatum Bulla striata Diodora gibberula Haminoea navicula Musculus discors Nudibranchia	Bivalvia
Bryozoa	Membranipora membranacea	Schizobrachiella sanguinea	Bryozoa	Brown bryozoa Pink spotted bryozoa White spotted bryozoa Creme bryozoa Bugula sp.
Echinodermata	Antedon bifida Asterias rubens Psammechinus miliaris		Amphiura chiajei Cidaris cidaris Ophiura ophiura	
Tunicata	Ascidiella aspersa Ciona intestinalis Corella parellogramma Diplosoma sp.	Botryllus schlosseri Polycarpa pomaria	Botryllus schlosseri Ascidiacea sp. Microcosmus polymorphus	Didemnum candidum Phallusia nigra Styela truncata

At the end of the experimental period, the non-metric MDS ordination shows both within- and between-site trends (Figure 4). The tight clustering of treatment levels for structures at Oban and Piran compared with a much wider spread of samples within the ordinations at Eilat indicates that differences in community composition between FF and R sites were greatest at Eilat.

SIMPER analysis indicated the contribution of species to the average dissimilarity between replicate artificial structures within each study area at each sampling event. In general, differences in species abundance accounted for the dissimilarity between artificial structures deployed at the FF and R sites for the three sampling events at Oban and Piran (Tables 5, 6, and 7). At Eilat, differences in the type of species accounted for the dissimilarity between communities on the structures at the FF and R sites over the experimental period. At Eilat, average similarity between structures at the FF site was higher than between structures at the R site for each sampling event, indicating a lower variability in community structure on structures deployed at the FF than at the R site. There were no differences in average similarity between artificial structures at the FF and R sites at Oban and Piran. SIMPER analysis was not performed on the Sitia data because of the loss of the R site.

At Oban, the hydroid *Obelia longissima* was the dominant species at the FF (91%) and R site (96%) after 1–2 months (Table 5). After 3–4 months, it had been replaced



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Figure 3. MDS plots showing temporal changes in community structure on artificial structures at the four study sites based on Bray—Curtis similarities from standardized, square-root transformed data for (a) Oban, (b) Piran, (c) Sitia, and (d) Eilat. Open symbols refer to the fish farm and closed to the reference site; 1–2 months (triangles), 3–4 months (inverted triangles), and 5–6 months (squares).

by the bivalve *Mytilus edulis* which dominated the community on the FF (46%) structures, and the tunicate *Ascidiella aspersa* accounted for a high proportion of the total biomass at the R site (32%; Table 6). Other species, including the non-native crustacean *Caprella mutica*, occurred predominantly at the FF (16%) and was absent from the R site. After 5–6 months, the community assemblage at the two treatment sites was similar in structure, and the dominant species was the tunicate *A. aspersa* (Table 7).

Table 4. Dissimilarities (%) between communities on artificial structures deployed at the fish farm (FF) and the reference sites (R) after 1, 3, and 5 months at the three study sites (square-root transformed data).

			Time (months)		
Site		1–2 R	3–4 R	5-6 R	
Oban Piran Eilat	FF FF FF	4.6 56.3*	33.3* 31.5* 68.3*	16.9 14.2* 73.3*	

ANOSIM results: * denotes significant difference between fish farm (FF) and reference site (R) at p < 0.05.

At Piran, the artificial structures were dominated by macroalgae (Chlorophyceae and Rhodophyceae) at the FF site (57%), whereas hydroids dominated the communities at the R site (67%) after 1–2 months (Table 5). After 3–4 months, the community was divided between the macroalgae *Polysiphonia* sp. and *Antithamnion* sp., the bryozoan

Stress: 0.06

Stress: 0.11

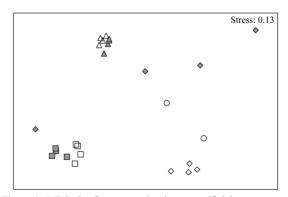


Figure 4. MDS plot for community data on artificial structures at the four study sites for 5–6 months after deployment based on Bray—Curtis similarities from standardized, square-root transformed data. Open symbols refer to the fish farm and closed to the reference site: Oban (triangles), Piran (squares), Sitia (circles), and Eilat (diamonds).

Table 5. SIMPER analysis of community structure from artificial structures deployed at Oban and Piran during the initial 1-2 months of deployment.

Fish farm					Referenc	e site		
Site	Taxon	Average abundance	%	Average similarity (%)	Taxon	Average abundance	%	Average similarity (%)
Oban	Hydroidea	91	98	93	Hydroidea	96	100	97
Piran	Algae	22	57	91	Hydroidea	49	67	94
	Hydroidea	8	20		Bryozoa	16	21	
	Bryozoa	7	16		Algae	8	9	

Average abundance (individuals per filter), similarity percentage, and overall average similarity between replicate samples from within each set of structures are listed.

Schizobrachiella sanguinea and the hydroid Campanopsis sp. on the artificial structures at the FF, whereas the bryozoan S. sanguinea dominated the community at the R site (Table 6). At the final sampling event (5–6 months), S. sanguinea dominated the community at the FF (80%) and R sites (92%). The macroalga Polysiphonia sp. and the hydroid Campanopsis sp. were still identified as characterizing species at the FF site, although their contribution to community structure was reduced (Table 7).

At Sitia, macroalgae (Chlorophyceae) dominated the fouling community in terms of coverage on the structures at the FF, and their abundance continued to increase between successive sampling periods. Rhodophytes were present initially on the structures, but declined in abundance over the experimental period. The two dominant colonial faunal species were the ascidian *Botryllus schlosseri* and an unidentified number of hydrozoans. Both these organisms showed maximal coverage on the structures after 4 months of deployment. After 5–6 months, the fouling community on the artificial structures was dominated, in

terms of biomass and abundance, by tube-dwelling polychaetes (Sabellidae and Serpulidae).

At Eilat, after 3–4 months the community structure was very different between artificial structures deployed at the FF and R sites (Table 6). The communities were dominated by the red macroalga *Jania* sp. at the FF site (78%), whereas hydroids dominated the R site (50%). Porifera (17%) and bryozoa (17%) were found at the R site, but were absent from the FF. After 5–6 months, *Jania* sp. continued to dominate the FF site (65%), but the poriferan *Mycale fistulifera* had increased in abundance on the artificial structures. At the R site, bryozoa replaced hydroids as the dominant group in the fouling community (Table 7).

Discussion

Biomass increase on the artificial structures deployed at the fish farms was greater than at the reference sites at Oban and Eilat, suggesting that caged mariculture may have

Table 6. SIMPER analysis of community structure from artificial structures following 3-4 months deployment at Oban, Piran, and Eilat.

	Fish farm				Reference site			
Site	Taxon	Average abundance	%	Average similarity (%)	Taxon	Average abundance	%	Average similarity (%)
Oban	Mollusca	43	46	87	Tunicata	30	32	81
	Crustacea	15	16		Hydroidea	28	26	
	Hydroidea	15	15		Mollusca	22	17	
	Tunicata	13	13		Polychaeta	7	6	
	Bryozoa	9	7		Bryozoa	7	6	
Piran	Bryozoa	37	36	85	Bryozoa	65	72	82
	Algae	31	33		Hydroidea	18	16	
	Hydroidea	27	26		Algae	9	7	
Eilat	Algae	54	78	76	Hydroidea	34	50	63
	Tunicata	12	13		Porifera	11	17	
					Bryozoa	12	17	
					Tunicata	14	14	

Average abundance (individuals per filter), similarity percentage, and overall average similarity between replicate samples from within each set of structures are listed.

Table 7. SIMPER analysis of community structure from artificial structures following 5-6 months deployment at Oban, Piran, and Eilat.

	Fish farm				Reference site			
Site	Taxon	Average abundance	%	Average similarity (%)	Taxon	Average abundance	%	Average similarity (%)
Oban	Tunicata	47	48	80	Tunicata	46	51	86
	Mollusca	32	29		Mollusca	28	28	
	Hydroidea	7	8		Hydroidea	10	8	
	Polychaeta	6	7		Polychaeta	8	8	
Piran	Bryozoa	82	80	94	Bryozoa	95	92	97
	Algae	11	9					
	Hydroidea	5	5					
Eilat	Algae	50	65	84	Bryozoa	34	40	37
	Porifera	23	25		Porifera	25	29	
					Mollusca	18	21	
					Tunicata	12	10	

Average abundance (individuals per filter), similarity percentage, and overall average similarity between replicate samples from within each set of structures are listed.

provided an enhanced food supply to epibiotic communities. This supports the results of an earlier associated study, using analysis of stable isotope ratios, conducted at the same sites as the present study (Lojen et al., 2003), which concluded that a proportion of the diet of the epibiotic communities, particularly at Eilat, was associated with nitrogen derived from the fish farm. Enhanced plankton stimulated by elevated nutrient levels in the close vicinity of the mariculture operation, however, may also play an important role in the diet. At Piran, hydrodynamic studies determined that the reference site was located within the radius of influence of the caged mariculture operation (~200 m; Malačič and Forte, 2003). The significantly lower biomass on the structures at the fish farm than at the reference site may have been caused by the uptake of particulates derived from the fish farm, as well as phyto- and zooplankton by the fouling organisms on the cage netting and associated structures, and/or the hydrodynamics adjacent to the cages, which may have reduced the proportion of food available to the epibiota on the artificial structures. The greater biomass on the structures at Piran than at the other study sites, irrespective of the distance to the mariculture operation, supports the results of other studies that have highlighted the highly productive, eutrophic nature of the Adriatic Sea (Bombace, 1989; Badalamenti et al., 1992).

A significant difference in community assemblage was observed between structures deployed adjacent to the fish farm and reference sites, particularly at Piran and Eilat. The difference in community assemblage was caused by a variation in number of species and abundance of the dominant species. At Piran and Eilat, macroalgae dominated the community assemblages at the fish farm but not at the reference site. The increased biomass of macroalgae may be explained by either reduced grazing pressure and/or increased growth rates at the fish farm site. Carnivorous

wild fish are attracted to fish farms in large numbers to feed on the particulate material released from cages (McDougall and Black, 1999; Dempster et al., 2002; ES, unpublished) and may indirectly lower the grazing pressure on macroalgae by reducing the number of herbivorous species in the vicinity of a fish farm. In addition, studies have measured elevated algal growth rates supported by dissolved inorganic nutrients released by the fish farms (Troell et al., 1997; Chopin et al., 1999). At Eilat, the increase in species number at the fish farm site also suggests that the levels of particulate matter derived from the farm support a greater abundance of heterotrophic species than the background levels of organic material in the northern region of the Gulf of Aqaba. However, the fewer species at the reference site than at the fish farm site may be related to increased disturbance to the artificial structures by grazers, particularly herbivorous fish and echinoderms, which have a significant effect on hard-substratum benthic communities (Goren, 1979; Russ, 1980). Grazing pressure was not measured in this study.

In contrast to the situation at Eilat, the community assemblage at Oban was dominated by heterotrophic filter-feeders throughout the study, and similar community assemblages developed on the artificial structures at the fish farm and reference sites. The west coast of Scotland has relatively nutrient-rich coastal waters, compared with the highly oligotrophic waters of the Gulf of Aqaba. This may have provided the epibiota on the structures at the reference site with sufficient nutrition to maintain a diverse fouling community. Stirling and Okumus (1995) found growth rates to be similar in the mussel *Mytilus edulis* grown adjacent to caged salmon culture and at a reference location on the west coast of Scotland, although mussels grown at the salmon farms tended to retain their dry meat weight during winter better than those grown at the reference site.

Studies have found that dissolved nutrients derived from fish farms are typically retained in measurable quantities around fish cages in areas of low dispersal (e.g. the Mediterranean; Pitta et al., 1998). In highly dispersive environments (e.g. the Bay of Fundy), dissolved nutrients are undetectable above background levels within a short distance of the fish farm (Wildish et al., 1993). At Piran the current measurements were relatively high for the Mediterranean, and the rapid dispersion of the dissolved nutrients released from the fish farm may be related to the reduced growth rates of macroalgae observed at the reference site. Conversely, the low residual current speeds at Eilat may have prevented the dissolved nutrients from reaching the reference site before assimilation by the pelagic auto- and heterotrophic community.

Similarly, dispersal of particulate material is highly dependent on the nature of an environment and the size of individual particles (Cromey et al., 2002). In general, uneaten feed is typically confined to a distance of <25 m from the cage group, although faecal particles which generally have a slower settling velocity will disperse more widely. This is particularly the case for the fine faecal material voided from sea bream and sea bass. For a 25-m deep site with a mean current speed of 10–12 cm s⁻¹ in a Mediterranean oligotrophic area, faecal material has been detected 1 km from the farm (Sara et al., 2004). The low residual current speeds recorded at Eilat suggest that this study site is the least dispersive site of those studied, and that neither uneaten feed nor faecal material would be able to reach the reference site. Food availability, therefore, may be an important contributing factor in the significant differences in community assemblage between the fish farm and reference site.

A significant difference in community structure was observed between the three sampling periods. Initially, autotrophs dominated the community assemblage on the artificial structures at the fish farm sites at Piran, Sitia, and Eilat. At Oban, macroalgae typically constituted <1% of the total fouling biomass on the artificial structures. In subtidal environments, light is a major consideration influencing the development of algal propagules into germlings (see reviews of Richmond and Seed, 1991; Hughes et al., 2005). Light attenuation is relatively rapid in coastal waters in the NE Atlantic compared with the Mediterranean and Red Sea, and may have contributed to the low biomass of macroalgae recorded on the structures at Oban.

After 5–6 months, the dominant groups on the artificial structures at the four study sites were heterotrophic filter-feeders, with the exception of the structures deployed close to the fish farm at Eilat, where macroalgae continued to dominate the fouling community. The dominant heterotrophic filter-feeders included species known to assimilate organic-rich detritus (e.g. particulate material derived from fish farms) including tunicates (Ribes *et al.*, 1998), bivalve molluscs (Bayne and Hawkins, 1992), and poriferans (Reiswig, 1971; Pile *et al.*, 1996). Bryozoans were also

a dominant species at Piran and Eilat. However, it is unknown whether non-living detritus forms a significant part of the natural diet of any bryozoan. These organisms typically dominate subtidal assemblages for reasons including superior competitive ability (e.g. tunicates and bryozoans), extended longevity and prolonged larval lifespan (e.g. mussels), and/or strong defensive responses (e.g. sponges; see the review of Richmond and Seed, 1991), and frequently dominate the surfaces of artificial reefs throughout Europe after the first year of deployment (Riggio, 1989; Jensen *et al.*, 1994; Relini *et al.*, 1994; Ardizzone *et al.*, 1996).

Seasonal variation in larval availability (Turner and Todd, 1993) and the location of the breeding population (Carlon and Olsen, 1993) influenced the community assemblage on the artificial structures deployed in the present study. This was highlighted at Oban by the non-native caprellid amphipod *Caprella mutica* (Willis *et al.*, 2004) which colonized the structures at the fish farm site in high densities after 3–4 months (September/October) because of the presence of a large breeding population on the fish farm throughout summer. However, after 5–6 months, the short longevity of the breeding season (May–October) and lifespan (~60 days) meant that the abundance of *C. mutica* on the structures had dropped significantly (Cook *et al.*, 2004).

Most studies to date have assessed the influence of caged mariculture on the community assemblage of softsediment benthic communities in limited geographical ranges. This study provides results of the influence of caged mariculture on early development of hard-substrata fouling communities, over a wide geographical range. It appears that caged mariculture, through the provision of an enhanced food supply, may increase the biomass of fouling communities, particularly in oligotrophic regions, and may have a greater influence on community structure in regions of low dispersion. In theory, for biofouling communities to be successful in reducing the environmental impact of caged fish culture, the position of the artificial structures relative to nutrient availability, light intensity, waste particle-settling, proximity to breeding populations, longevity, grazing pressure, and predation should be considered carefully in order to maximize the effectiveness of the "biofilter" in removing fine particulates derived from fish farms and dissolved nutrients from the water column. In practice, the scale of the biofiltering material required for significant retention of nutrient wastes over the whole industry is likely to remain extremely large, and an impractical number of filters would be needed to allow the application of this technology at a commercial scale (Cook et al., 2004). However, biofilters could be used in specific cases where even a small reduction in loadings could be critical for the health of the environment, or the growth of commercially valuable species could assist in reducing the waste and provide a co-harvesting incentive for the industry to adopt a more environmentally sustainable approach to cage mariculture.

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