IMPACT OF ARTIFICIAL LIGHT ON BEHAVIOURAL PATTERNS OF COASTAL FISHES OF CONSERVATION INTEREST

VPLIV UMETNE SVETLOBE NA VEDENJSKE VZORCE OBALNIH RIB NARAVOVARSTVENEGA POMENA

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ABSTRACT

The effects of artificial light of variable intensity and wavelength were investigated on aggregation, phototaxis and photokinesis in the blue damselfish *Chromis chromis* L., the brown meagre *Sciaena umbra* L., the peacock wrasse *Symphodus tinca* L. and the white seabream *Diplodus sargus* L. Overall, the brown meagre was the most affected by the presence of artificial light. The other three species did not react conspicuously to light exposure. The results fit into the ecological classification of species according to their visual behaviour patterns towards artificial light, and show that the rationalisation of artificial light emissions in the underwater environment would help to improve the quality of management and the effectiveness of conservation policies in coastal and marine protected areas.

IZVLEČEK

Avtorji članka so preučevali vplive umetne svetlobe različnih intenzitet in valovnih dolžin na agregacijo, fototakso in fotokinezo pri črniku *Chromis chromis* L., konju *Sciaena umbra* L., pisani ustnači *Symphodus tinca* L. in šargu *Diplodus sargus* L. Izkazalo se je, da je za umetno svetlobo najbolj občutljiv konj, medtem ko pri preostalih treh vrstah ni bilo videti, da bi se odzivale nenavadno nanjo. Rezultati raziskave se ujemajo z ekološko klasifikacijo vrst glede na njihove vidne vedenjske vzorce med izpostavljenostjo umetni svetlobi in kažejo, da bi z racionalizacijo sevanja umetne svetlobe v podvodnem okolju izboljšali kakovost upravljanja in učinkovitost naravovarstvenih ukrepov v obalnih in morskih zaščitenih območjih.

1. INTRODUCTION

Most fish depend on photoreception in order to perform activities that are crucial for survival (e.g. Lythgoe, 1979). Behavioural patterns are often differentiated throughout the twenty-four hour cycle. The activities performed in different periods of the day may depend on each species' visual characteristics (Helfman, 1993). Activity rhythms, behavioural patterns and visual system of most species are therefore strictly correlated, and depend on both phylogenetic traits and ecological conditions of life. Species that have evolved in similar environments, or that have similar lifestyles, tend to show common traits in their visual adaptations (e.g. Land & Nilsson, 2002). A primary role in shaping visual system and behaviour of different groups of fish is played by their inter-specific trophic relations (Hobson et al., 1981; Pankhurst & Hilder, 1998). In each fish community, we can recognise strictly diurnal species (e.g. *Chromis chromis* L., *Symphodus tinca* L.), strictly nocturnal species (e.g. *Sciaena umbra* L., *Scorpaena porcus* L.) and species characterised by more flexible circadian behavioural patterns (e.g. *Diplodus sargus* L., *Sparus auratus* L.). Broadly speaking, diurnal species are well-adapted to the exposure of a wide range of light intensities throughout the whole visual spectrum (conventionally referred to the human range, but see Hawryshyn, 2003). This is usually associated to a low reactivity to light stimuli and to a good tolerance for high light intensities. On the other hand, nocturnal species can easily detect the presence of low-to-very-low light sources, and they are particularly sensitive to the shorter wavelengths of the visual spectrum (violet, blue, green-blue). The level of tolerance to light exposure is reduced, and they usually tend to move away from the light. The exposure to light stimuli, either natural or artificial, can therefore induce diverse and conspicuous reactions in fish (Ben-Yami, 1976). The type of response is often associated to each species' feeding habits. In most cases, fish that are attracted by strong lights have diurnal habits, and they are often planktivorous, detritivorous or grazers (Ben-Yami, 1976; Marchesan et al., 2003). Most other species tend to prefer medium-to-low lights and to keep at some distance from the light source (Ben-Yami, 1976; Kawamura, 1986; Beltestad & Misund, 1988). Such a distance is higher for strictly nocturnal species, whereas it is shorter for crepuscular species that show peaks of activity during the twilight periods. In most cases, such species are characterised by carnivorous habits (Ben-Yami, 1976; Marchesan et al., 2003).

Coastal fish communities are among the most sensitive to human disturbance, as many anthropic activities are concentrated along the coast, for instance small scale fishing with lights, coastline traffic and public illumination, lighthouses and harbour lights, light and sound performances in tourist areas. Hence, the evaluation of the impact of human activities on coastal fishes of conservation interest is of the utmost importance for the effective management of marine protected areas. It is apparent that such areas should be free from 'photopollution' (Verheijen, 1985; Witherington, 1997), but this does not mean that all activities implying the use of light should be avoided, as long as they are calibrated on the level of tolerance of the most sensitive species.

In this study, the behavioural effects of artificial light were investigated in four fish species of conservation interest: the blue damselfish *C. chromis* L., the brown meagre *S. umbra* L., the peacock wrasse *S. tinca* L. and the white seabream *D. sargus* L. The aim of the study was to determine how levels of aggregation, phototaxis and photokinesis of the experimental fish were affected by lights of variable intensity and wavelength. Such investigations were performed in order to define the specific level of disturbance associated to the emission of artificial light, and thus to determine the light levels that could be tolerated by the fish community living inside a marine reserve.

2. MATERIALS AND METHODS

All observations were carried out at the Department of Biology of the University of Trieste between October 2002 and November 2003. The experimental fish were obtained from wild caught stocks kept at the Aquarium of Piran (Slovenia). For each species, groups of 10 adults of medium size were tested.

All experiments were carried out in a grey fibreglass tank (L x W x H: 320 x 40 x 60 cm). A transparent glass window (W x H: 30 x 50 cm), uncovered only during the experiments, was present at one of the short sides of the rectangular tank. The tank was divided into 5 sections, the closest to the light source was called E, the farthest A.

The tank was filled with approximately 700 l artificial seawater and fitted with closed circuit filtering and water re-circulating system. Water temperature was maintained in the 18-22°C range, salinity in the 30-34 ‰ range. Before being tested, fish were left in the experimental tank for at least one week to acclimate, and were subjected to a 12 L:12 D photoperiod (Light from 06:00 to 18:00; Dark from 18:00 to 06:00). Ambient illumination at water-level was about 20 $\mu Es^{-1}m^{-2}$ in light conditions, provided by Philips type 94 fluorescent tubes matching the solar spectrum, and $8x10^{-3}$ $\mu Es^{-1}m^{-2}$ in dark conditions.

Both before and during the experiments, fish were fed every two or three day's ad libitum on chopped *Atherina* sp. At the end of the tests, the fish were either released in the open sea or used for other investigations.

The experimental light beam was provided by a Strand Harmony 22 illuminator equipped with a 1000 W halogen lamp. The illuminator was placed in front of the glass window, at one meter distance. The diffused light beam was regulated in order to exactly fit the window.

Light intensity was varied with a rheostat in discrete steps. Eight levels of irradiance were tested: (1) 0.2 $\mu Es^{-1}m^{-2}$, (2) 4 $\mu Es^{-1}m^{-2}$, (3) 10 $\mu Es^{-1}m^{-2}$, (4) 20 $\mu Es^{-1}m^{-2}$, (5) 30$\mu Es^{-1}m^{-2}$, (6) 41$\mu Es^{-1}m^{-2}$, (7) 53$\mu Es^{-1}m^{-2}$, (8) 68$\mu Es^{-1}m^{-2}$. The intensity was always kept well within the fish photopic vision and tolerance limits. It spans the range from crepuscular to full day light in coastal waters (Clarke & Denton, 1962; Ali, 1971).

Light colour was varied throughout the visual spectrum by placing LEE Filters monochrome gelatine sheets in front of the lamp. Six colours were tested: (1) violet (peak at approx. 410 nm), (2) blue (peak at approx. 460nm), (3) green (peak at approx. 525nm), (4) yellow (peak at approx. 580nm), (5) orange (peak at approx. 600nm), (6) red (peak at approx. 650nm). For all colours, irradiance was regulated at a standard of 4 $\mu Es^{-1}m^{-2}$, as this was the maximum intensity that could be reached by the colour with highest absorbance (blue filter) and still within the range of colour vision.

Light irradiance measurements were made with a Li-Cor radiometer equipped with a LI-192SA PAR (photosynthetically active radiation) underwater quantum sensor, sensitive to $0.5x10^{-3}$ $\mu E\ s^{-1}\ m^{-2}$. The sensor was placed in mid-water, at 30 cm distance from the glass window. A light gradient was present along the tank, and light intensity was attenuated of about 70% at 300 cm distance from the glass window.

Two sets of experiments were carried out, following the protocols described hereby.

First set of experiments: reactions to light stimuli of variable intensity. For each species, two experiments were performed. Three replicate trials were conducted for each experiment.

In the first experiment (LH), light intensity was progressively increased from the lowest (1) to the highest (8) level over a time span of 4 hours. In the second experiment (HL), light intensity was progressively decreased from the highest to the lowest level, again over a span of 4 hours.

Each light condition was kept for 30 minutes to allow habituation of the fish. Recordings were carried out during the first 20 minutes of exposure to each illumination level. All experimental sessions started at 18:00 and ended at 22:00. For each species, a total of 960 minutes of videotapes were analysed.

Second set of experiments: reactions to light stimuli of variable wavelength. Again, two experiments were performed for each species. Three replicate trials were conducted for each experiment.

In the first experiment (SL), light colour was progressively shifted from the shorter (violet) to the longer (red) wavelengths of the visual spectrum, testing 6 colours over a span of 3 hours. In the second experiment (LS), light colour was progressively shifted from the longer to the shorter wavelengths of the visual spectrum, again testing 6 colours over a span of 3 hours.

Each light condition was kept for 30 minutes to allow habituation of the fish. Recordings were carried out during the first 20 minutes of exposure to each level of illumination. All experimental sessions started at 18:00 and ended at 21:00. For each species, a total of 840 minutes of videotapes were analysed.

Behavioural patterns were analysed from remote video-recorded sessions. All recordings were performed with a SONY SSC-DC50AP colour video-camera with minimum sensitivity of 1 lux. Videotapes were preliminary observed at 9X speed, to obtain a first qualitative description of each session. Then a temporal sequence of 21 frames, randomly chosen within 1 minute intervals throughout the session, was analysed in detail.

The following parameters were considered: (1) mean nearest neighbour distance (MNND), as a proportion of fish total length, to determine the level of aggregation of the group of fish, (2) mean percentage of fish in the area closest to (E) and farther from (A) the light source, to define the degree of attraction to or repulsion from light, (3) mean percentage of fish still, to determine fish activity levels and thus degree of inhibition.

Statistical analysis was performed using the statistical package Statistica 5.1. Only non-parametric statistics were used. Mean values were given ± one standard deviation. Significance was set at probability P=0.05.

3. RESULTS

Reactions to light stimuli of variable intensity

The blue damselfish *C. chromis* L. was moderately affected by changes in light intensity, and it was especially attracted by strong lights. Individuals maintained a positive phototaxis even when light intensity was experimentally decreased. In all cases, the level of aggregation was rather low, and a high percentage of fish tended to keep still.

During both experiments, there were no significant differences in the degree of aggregation of the group of fish at different light intensities (Fig. 1a, HL & LH, Kruskal-Wallis test, d.f.=7, NS). Fish showed a higher aggregation with an increasing light intensity only at low illumination levels (HL vs LH, levels 1-3, Mann-Whitney U test, n=3, P<0.01). When light intensity was progressively increased, fish tended to keep close to the light source when the illumination was low (level 1-3) and to move away from it when it became stronger, whereas the differences in the phototactic reactions between illumination levels were less pronounced,

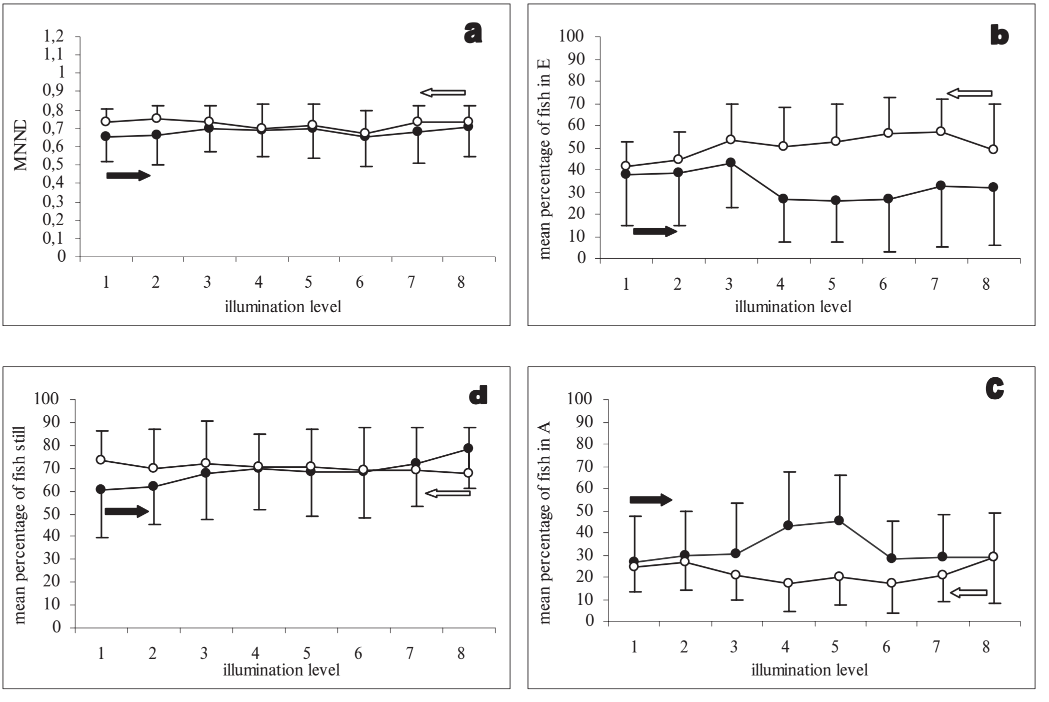

Figure 1: Blue Damselfish *C. chromis* L.
Effects of light intensity variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment LH: illumination progressively increased from the Lowest (1) to the Highest (8) level. Open circles and arrows indicate experiment HL: illumination progressively decreased from the Highest (8) to the Lowest (1) level. Values given as means (n=3), bars ± one standard deviation. Levels of irradiance tested: (1) 0.2 µEs-1m-2, (2) 4 µEs-1m-2, (3) 10 µEs-1m-2, (4) 20 µEs-1m-2, (5) 30µEs-1m-2, (6) 41µEs-1m-2, (7) 53µEs-1m-2, (8) 68µEs-1m-2.
Slika 1: Črnik C. chromis L.
Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjih sosedov (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment LH: svetloba se je postopoma povečevala od L (najšibkejše - 1) do H (najmočnejše - 8). Prazni krogci in puščice ponazarjajo eksperiment HL: svetloba se je postopoma zmanjševala od H (najmočnejše - 8) do L (najšibkejše - 1). Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Ravni testiranega izžarevanja: (1) 0.2 µEs-1m-2, (2) 4 µEs-1m-2, (3) 10 µEs-1m-2, (4) 20 µEs-1m-2, (5) 30µEs-1m-2, (6) 41µEs-1m-2, (7) 53µEs-1m-2, (8) 68µEs-1m-2.

although still significant, with a decreasing light intensity (Fig. 1b,c, LH and HL, Kruskal-Wallis test, d.f.=7, P<0.01). Fish were significantly more attracted to light when the illumination was strong at first and then progressively diminished (HL vs LH, Mann-Whitney U test, n=3, P<0.01). Switching from low to high illumination levels, fish tended to be moderately active at first, and to become stiller as the experiment progressed (Fig. 1d, LH, Kruskal-Wallis test, d.f.=7, P<0.01). No variations in the level of photokinesis were registered when light intensity was progressively decreased (Fig. 1d, HL, Kruskal-Wallis test, d.f.=7, NS). Fish activity was significantly more inhibited by a progressive increase in light intensity (HL vs LH, Mann-Whitney U test, n=3, P<0.01).

The brown meagre *S. umbra* L. was strongly reactive to the presence of an illuminated field during both experiments, independent of the light intensity. Overall, fish tended to aggregate as far as possible from the light source, and to keep still in such a position. However, it is interesting to note that during the low-to-high illumination experiment, fish showed an increase in the aggregation and inhibition levels, and a higher negative phototaxis, when light intensity was varied from crepuscular to diurnal levels (lev. 1-2 to 3-4).

The group of fish was characterised by high MNNDs during both experiments. In particular, fish showed a pronounced aggregation when they were exposed to strong lights at the beginning of the experiment, and when light intensity varied from crepuscular to diurnal values (Fig. 2a, HL and LH, Kruskal-Wallis test, d.f.=7, P<0.01). Overall, the presence of strong illumination followed by a decrease in light intensity induced higher aggregation of the fish group (HL vs LH, Mann-Whitney U test, n=3, P<0.01). At all light levels, fish were dramatically repulsed by the presence of a light source (Fig. 2b, c, HL and LH, Kruskal-Wallis test, d.f.=7, P<0.01). Overall, the level of negative phototaxis was higher during the high-to-low illumination experiment (HL vs LH, Mann-Whitney U test, n=3, P<0.01). All fish tended to keep still throughout the high-to-low experiment (Fig. 2d, HL, Kruskal-Wallis test, d.f.=3, NS). When light was progressively increased, fish showed a peak in their inhibition levels in the central part of the experiment (levels 3-5) (Fig. 2d, LH, Kruskal-Wallis test, d.f.=7, P<0.01). Overall, the degree of inhibition was, however, higher when light intensity was progressively decreased (HL vs LH, Mann-Whitney U test, n=3, P<0.01).

The peacock wrasse *S. tinca* L. was only slightly affected by changes in light intensity. During both experiments, fish tended to show moderate aggregation and to keep still in the proximity of the light source.

During both experiments, the group of fish showed a slight tendency to increase the aggregation as the experiment went on (Fig. 3a, LH and HL, Kruskal-Wallis test, d.f.=7, P<0.01). Overall, the group was more cohered when light intensity was progressively increased (LH vs HL, Mann-Whitney U test, n=3, P<0.01). Fish were strongly attracted to light during both experiments, and the differences among light levels did not show any specific trend, although still significant (Fig. 3b,c, LH and HL, Kruskal-Wallis test, d.f.=7, P<0.01). However, fish were more attracted to light during the low-to-high experiment (LH vs HL, Mann-Whitney U test, n=3, P<0.01). Levels of inhibition were high during both experiments, and both within and between experiment differences were not pronounced (Fig. 3d, LH and HL, Kruskal-Wallis test, d.f.=7, P<0.05; LH vs HL, Mann-Whitney U test, n=3, P<0.05).

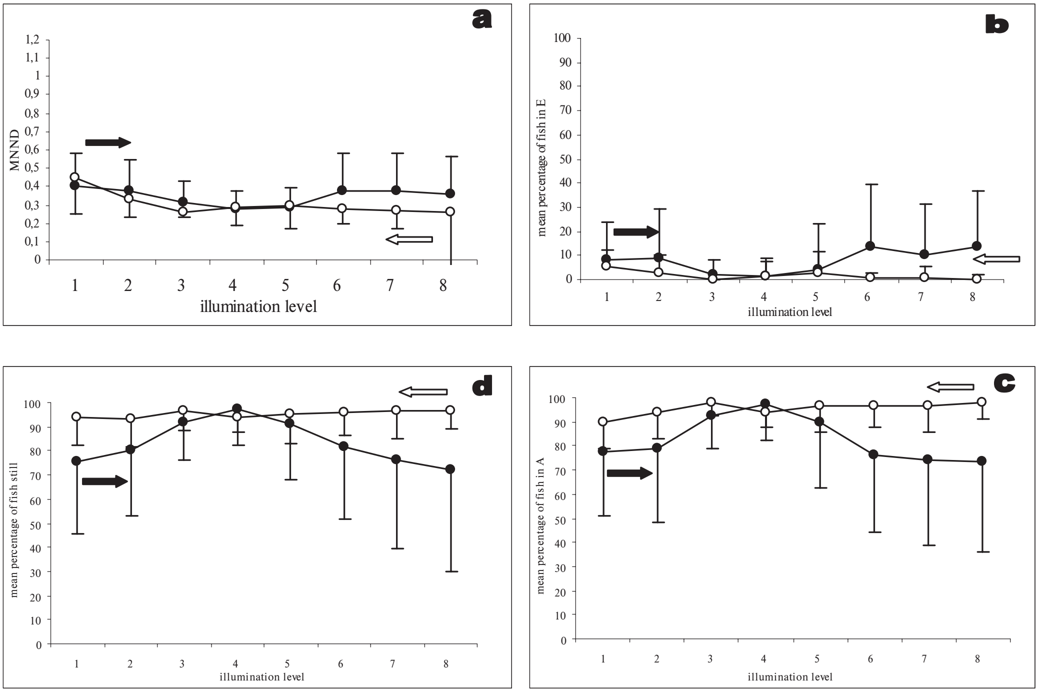

Figure 2: Brown Meagre *S. umbra* L.
Effects of light intensity variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment LH: illumination progressively increased from the Lowest (1) to the Highest (8) level. Open circles and arrows indicate experiment HL: illumination progressively decreased from the Highest (8) to the Lowest (1) level. Values given as means (n=3), bars ± one standard deviation. Levels of irradiance tested: (1) 0.2 μEs-1m-2, (2) 4 μEs-1m-2, (3) 10 μEs-1m-2, (4) 20 μEs-1m-2, (5) 30μEs-1m-2, (6) 41μEs-1m-2, (7) 53μEs-1m-2, (8) 68μEs-1m-2.
Slika 2: Konj S. umbra L.
Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjih sosedov (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment LH: svetloba se je postopoma povečevala od L (najšibkejše - 1) do H (najmočnejše - 8). Prazni krogci in puščice ponazarjajo eksperiment HL: svetloba se je postopoma zmanjševala od H (najmočnejše - 8) do L (najšibkejše - 1). Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Ravni testiranega izžarevanja:: (1) 0.2 μEs-1m-2, (2) 4 μEs-1m-2, (3) 10 μEs-1m-2, (4) 20 μEs-1m-2, (5) 30μEs-1m-2, (6) 41μEs-1m-2, (7) 53μEs-1m-2, (8) 68μEs-1m-2.

The white seabream *D. sargus* L. was influenced by changes in light intensity during both experiments, although the reactions were not always pronounced. Overall, fish tended to show moderate aggregation, and to keep active at some distance from the light source.

Levels of aggregation were higher when fish were exposed to low lights at the beginning of the experiment, whereas no specific trends were recognisable during the high-to-low experiment, although the variations were still significant (Fig. 4a, LH and HL, Kruskal-Wallis test, d.f.=7, P<0.01). Comparing the two experiments, group cohesion was higher when fish experienced low illumination conditions first (LH vs HL, Mann-Whitney U test, n=3, P<0.01). Fish tended to be progressively more attracted to the illuminated area as light intensity increased (Fig.

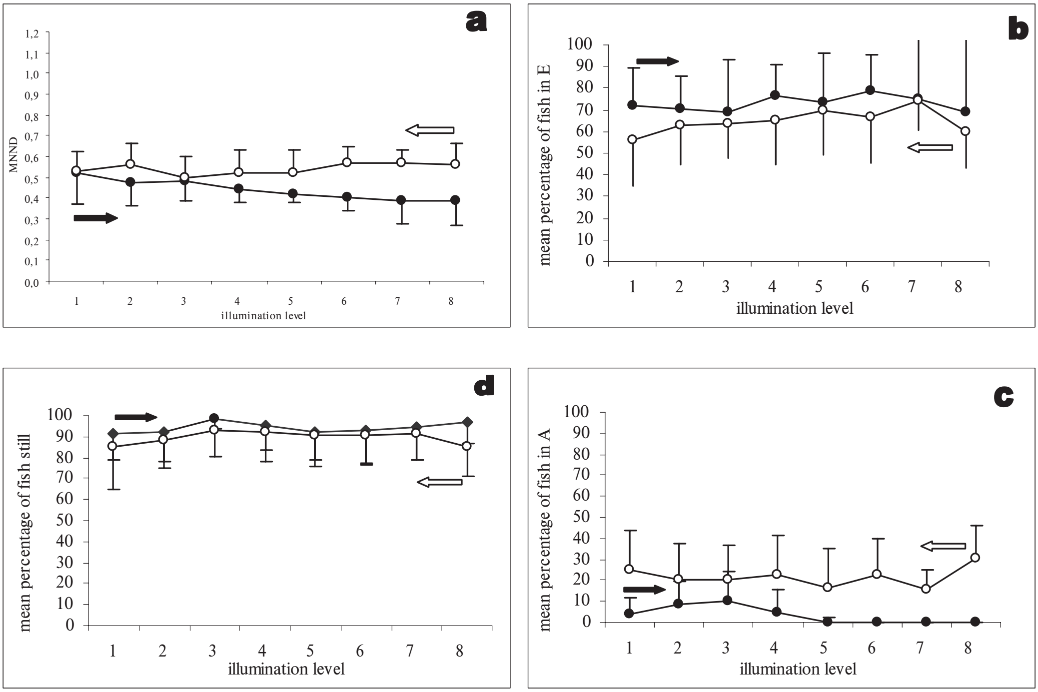

Figure 3: Peacock Wrasse *S. tinca* L.
Effects of light intensity variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment LH: illumination progressively increased from the Lowest (1) to the Highest (8) level. Open circles and arrows indicate experiment HL: illumination progressively decreased from the Highest (8) to the Lowest (1) level. Values given as means (n=3), bars ± one standard deviation. Levels of irradiance tested: (1) 0.2 µEs-1m-2, (2) 4 µEs-1m-2, (3) 10 µEs-1m-2, (4) 20 µEs-1m-2, (5) 30µEs-1m-2, (6) 41µEs-1m-2, (7) 53µEs-1m-2, (8) 68µEs-1m-2.
Slika 3: Pisana ustnača S. tinca L.
Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjih sosedov (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment LH: svetloba se je postopoma povečevala od L (najšibkejše - 1) do H (najmočnejše - 8). Prazni krogci in puščice ponazarjajo eksperiment HL: svetloba se je postopoma zmanjševala od H (najmočnejše - 8) do L (najšibkejše - 1). Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Ravni testiranega izžarevanja:: (1) 0.2 µEs-1m-2, (2) 4 µEs-1m-2, (3) 10 µEs-1m-2, (4) 20 µEs-1m-2, (5) 30µEs-1m-2, (6) 41µEs-1m-2, (7) 53µEs-1m-2, (8) 68µEs-1m-2.

4b,c, LH, Kruskal-Wallis test, d.f.=7, P<0.01), whereas differences were less pronounced with a decreasing light intensity (Fig. 4b,c, HL, Kruskal-Wallis test, d.f.=7, P<0.05). However, comparing the two experiments, it is apparent that fish were more attracted to light when the illumination was strong at first and then progressively decreased (HL vs LH, Mann-Whitney U test, n=3, P<0.01). The level of inhibition was low in all cases, and tended to further decrease throughout both experiments (Fig. 4d, LH and HL, Kruskal-Wallis test, d.f.=7, P<0.01). At high illumination levels, fish were progressively more active if they had been exposed to low light intensity first (LH vs HL, Mann-Whitney U test, n=3, P<0.01).

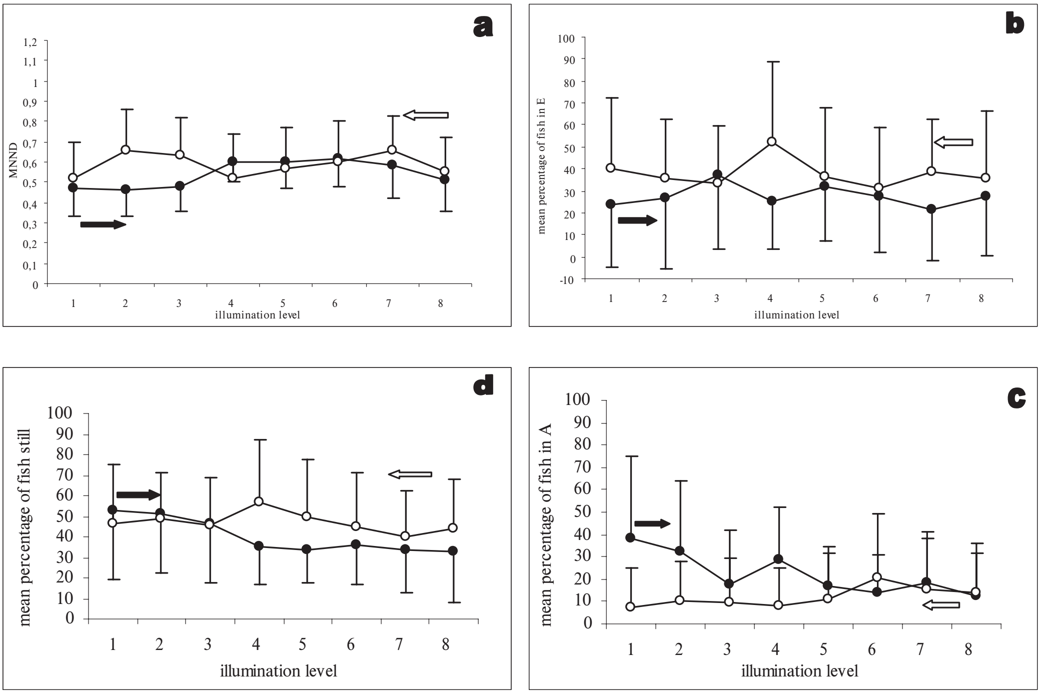

Figure 4: White seabream *D. sargus* L.
Effects of light intensity variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment LH: illumination progressively increased from the Lowest (1) to the Highest (8) level. Open circles and arrows indicate experiment HL: illumination progressively decreased from the Highest (8) to the Lowest (1) level. Values given as means (n=3), bars ± one standard deviation. Levels of irradiance tested: (1) 0.2 $\mu Es^{-1}m^{-2}$, (2) 4 $\mu Es^{-1}m^{-2}$, (3) 10 $\mu Es^{-1}m^{-2}$, (4) 20 $\mu Es^{-1}m^{-2}$, (5) 30$\mu Es^{-1}m^{-2}$, (6) 41$\mu Es^{-1}m^{-2}$, (7) 53$\mu Es^{-1}m^{-2}$, (8) 68$\mu Es^{-1}m^{-2}$.
Slika 4: Šarg D. sargus L.
Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjih sosedov (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment LH: svetloba se je postopoma povečevala od L (najšibkejše - 1) do H (najmočnejše - 8). Prazni krogci in puščice ponazarjajo eksperiment HL: svetloba se je postopoma zmanjševala od H (najmočnejše - 8) do L (najšibkejše - 1). Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Ravni testiranega izžarevanja:: (1) 0.2 $\mu Es^{-1}m^{-2}$, *(2) 4* $\mu Es^{-1}m^{-2}$, *(3) 10* $\mu Es^{-1}m^{-2}$, *(4) 20* $\mu Es^{-1}m^{-2}$, *(5) 30*$\mu Es^{-1}m^{-2}$, *(6) 41*$\mu Es^{-1}m^{-2}$, *(7) 53*$\mu Es^{-1}m^{-2}$, *(8) 68*$\mu Es^{-1}m^{-2}$.

Reactions to light stimuli of variable wavelength

The blue damselfish *C. chromis* L. was not particularly affected by the exposure to monochromatic lights of different wavelength, independent of the order of presentation. In general, the aggregation was low, the level of inhibition medium-to-high, and the attraction to the light source moderate.

There were no significant variations in the degree of aggregation either shifting light colour from violet to red or back (Fig. 5a, SL and LS, Kruskal-Wallis test, d.f.=7, P=NS). Similarly, there were no differences between the level of aggregation shown by the group of fish during the two experiments (SL vs LS, Mann-Whitney U test, n=3, P=NS). During the violet-to-red experiment, fish tended to be progressively less attracted to the light source as the test went on (Fig. 5b,c, SL, Kruskal-Wallis test, d.f.=7, P<0.01). The exposure to red light induced a repulsive reaction also during the red-to-violet experiment, but the level of attraction was medium and constant throughout the rest of the test (Fig. 5b,c, LS, Kruskal-Wallis test, d.f.=7, P<0.01). Overall, fish were slightly more attracted to light when the colour was shifted from red to violet (Fig. 5b,c, SL vs LS, Mann-Whitney U test, n=3, P<0.01). A high percentage of fish was still

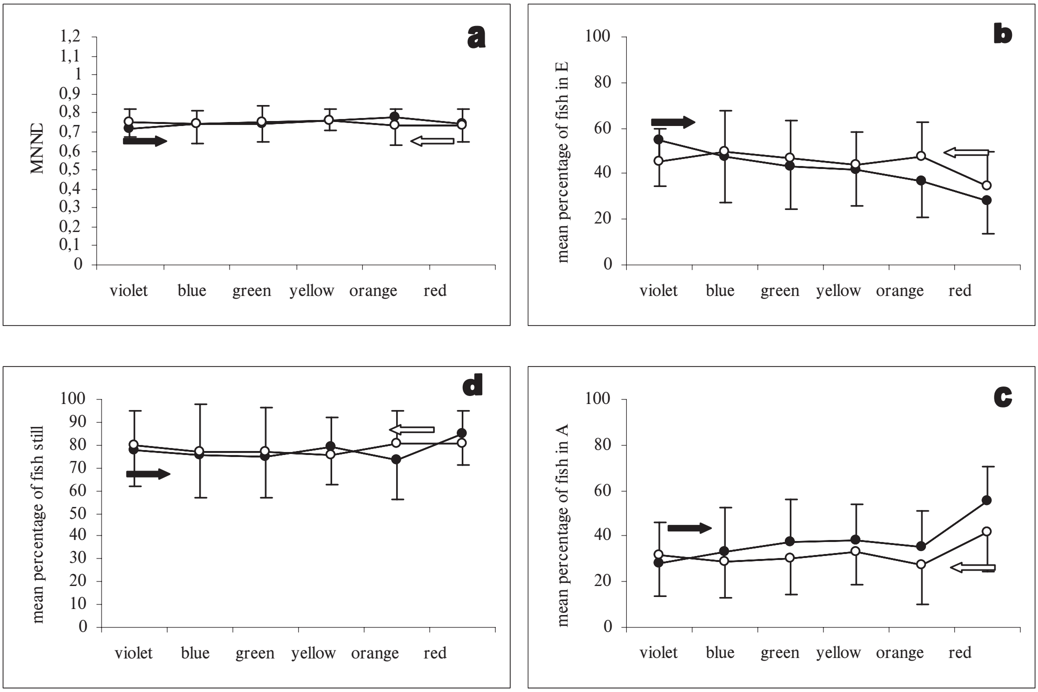

Figure 5: Blue Damselfish *C. chromis* L.

Effects of light colour variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment SL: light colour progressively shifted from the Shorter (violet) to the Longer (red) wavelengths of the visual spectrum. Open circles and arrows indicate experiment LS: light colour progressively shifted from the Longer (red) to the Shorter (violet) wavelengths of the visual spectrum. Values given as means (n=3), bars ± one standard deviation. Colours tested: (1) violet (peak at approx. 410 nm), (2) blue (peak at approx. 460nm), (3) green (peak at approx. 525nm), (4) yellow (peak at approx. 580nm), (5) orange (peak at approx. 600nm), (6) red (peak at approx. 650nm).

Slika 5: Črnik C. chromis L.

Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjega soseda (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment SL: svetla svetloba se je postopoma premikala od S (krajših – vijoličnih) do L (daljših – rdečih) valovnih dolžin vidnega spektra. Prazni krogci in puščice ponazarjajo eksperiment LS: svetla svetloba se je postopoma premikala od L (daljših – rdečih) do S (krajših-vijoličnih) valovnih dolžin vidnega spektra. Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Testirane barve: (1) vijolična (višek pri pribl. 410 nm), (2) modra (višek pri pribl. 460nm), (3) zelena (višek pri pribl. 525nm), (4) rumena (višek pri pribl. 580nm), (5) oranžna (višek pri pribl. 600nm), (6) rdeča (višek pri pribl. 650nm).

in all cases and during both experiments (Fig. 5d, LS, Kruskal-Wallis test, d.f.=7, P=NS; SL, Kruskal-Wallis test, d.f.=7, $P<0.05$; SL vs LS, Mann-Whitney U test, n=3, P=NS).

The brown meagre *S. umbra* L. was conspicuously influenced by monochromatic lights that induced overall a negative reaction. Fish tended to be especially repulsed by the shorter-wavelength colours (violet, blue and to a lesser extent green).

During both experiments, the cohesion was high in presence of violet, blue and green lights, whereas the MNND slightly increased with the other colours (Fig. 6a, SL and LS, Kruskal-Wallis test, d.f.=7, $P<0.01$). In general, fish were more aggregated when they were

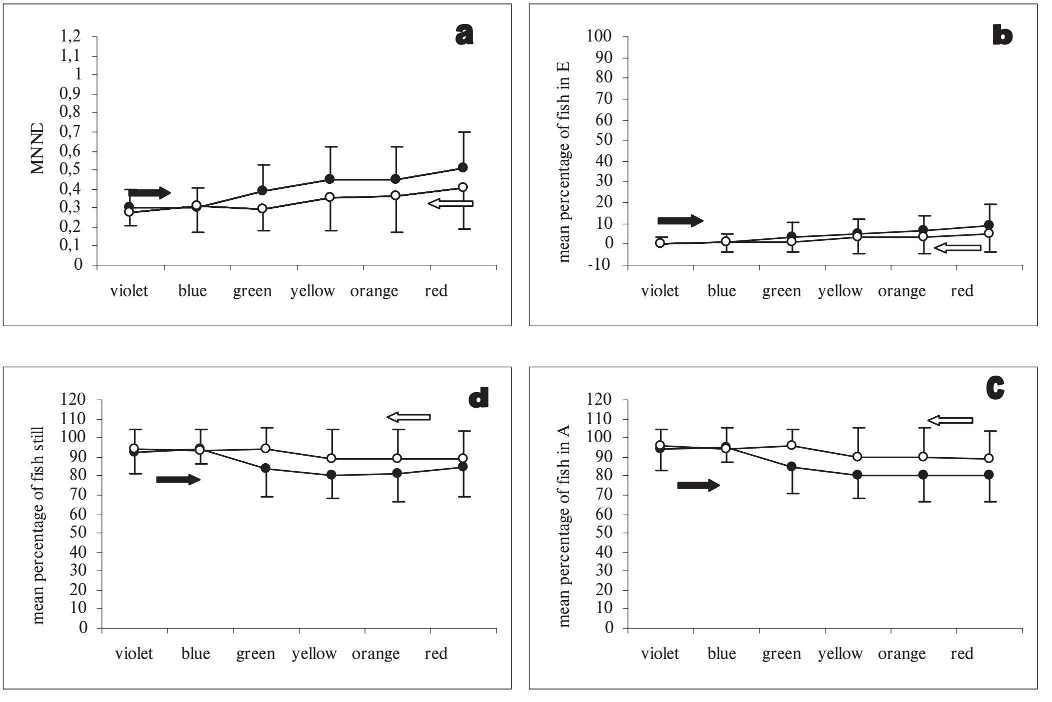

Figure 6: Brown Meagre *S. umbra* L.

Effects of light colour variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment SL: light colour progressively shifted from the Shorter (violet) to the Longer (red) wavelengths of the visual spectrum. Open circles and arrows indicate experiment LS: light colour progressively shifted from the Longer (red) to the Shorter (violet) wavelengths of the visual spectrum. Values given as means (n=3), bars ± one standard deviation. Colours tested: (1) violet (peak at approx. 410 nm), (2) blue (peak at approx. 460nm), (3) green (peak at approx. 525nm), (4) yellow (peak at approx. 580nm), (5) orange (peak at approx. 600nm), (6) red (peak at approx. 650nm).

Slika 6: Konj S. umbra L.

Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjih sosedov (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment SL: svetla svetloba se je postopoma premikala od S (krajših – vijoličnih) do L (daljših – rdečih) valovnih dolžin vidnega spektra. Prazni krogci in puščice ponazarjajo eksperiment LS: svetla svetloba se je postopoma premikala od L (daljših – rdečih) do S (krajših-vijoličnih) valovnih dolžin vidnega spektra. Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Testirane barve: (1) vijolična (višek pri pribl. 410 nm), (2) modra (višek pri pribl. 460nm), (3) zelena (višek pri pribl. 525nm), (4) rumena (višek pri pribl. 580nm), (5) oranžna (višek pri pribl. 600nm), (6) rdeča (višek pri pribl. 650nm).

exposed to red light (diurnal wavelengths) first (SL vs LS, Mann-Whitney U test, n=3, P<0.01). Violet and blue lights projected at the beginning of the experiment induced a particularly strong repulsion (Fig. 6b,c, SL, Kruskal-Wallis test, d.f.=7, P<0.01). During the second experiment, all colours appeared to evoke a constant and strong negative reaction (Fig. 6b,c, LS, Kruskal-Wallis test, d.f.=7, P<0.05). Long-to-medium-wavelength colours were significantly more repulsive when presented at the beginning of the experiment (SL vs

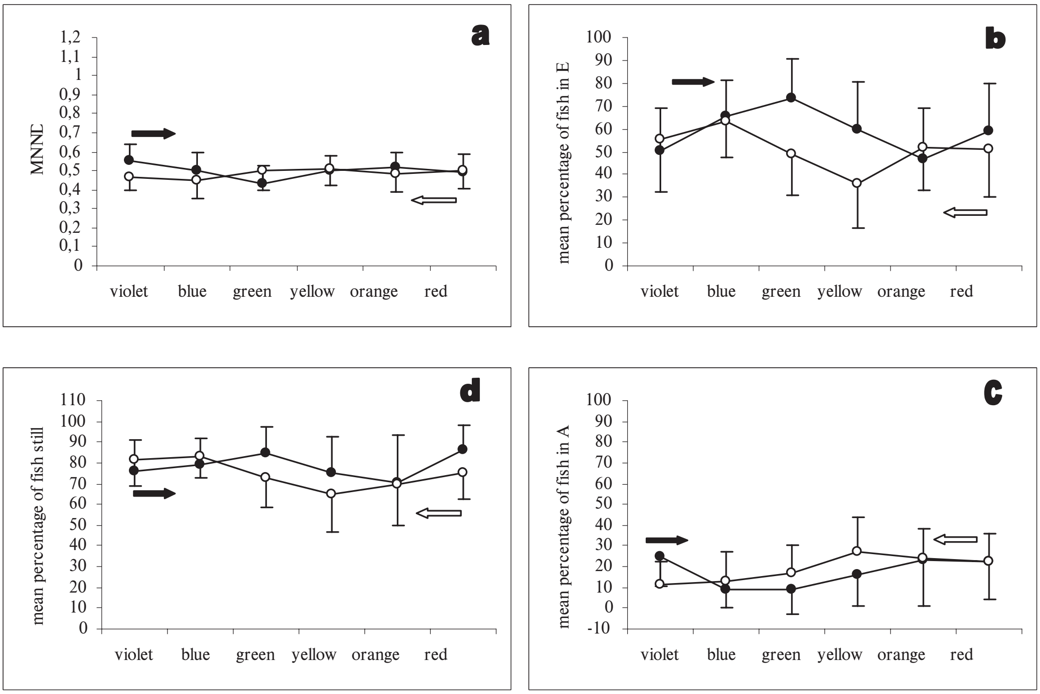

Figure 7: Peacock Wrasse *S. tinca* L.
Effects of light colour variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment SL: light colour progressively shifted from the Shorter (violet) to the Longer (red) wavelengths of the visual spectrum. Open circles and arrows indicate experiment LS: light colour progressively shifted from the Longer (red) to the Shorter (violet) wavelengths of the visual spectrum. Values given as means (n=3), bars ± one standard deviation. Colours tested: (1) violet (peak at approx. 410 nm), (2) blue (peak at approx. 460nm), (3) green (peak at approx. 525nm), (4) yellow (peak at approx. 580nm), (5) orange (peak at approx. 600nm), (6) red (peak at approx. 650nm).
Slika 7: Pisana ustnača S. tinca L.
Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjih sosedov (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment SL: svetla svetloba se je postopoma premikala od S (krajših – vijoličnih) do L (daljših – rdečih) valovnih dolžin vidnega spektra. Prazni krogci in puščice ponazarjajo eksperiment LS: svetla svetloba se je postopoma premikala od L (daljših – rdečih) do S (krajših-vijoličnih) valovnih dolžin vidnega spektra. Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Testirane barve: (1) vijolična (višek pri pribl. 410 nm), (2) modra (višek pri pribl. 460nm), (3) zelena (višek pri pribl. 525nm), (4) rumena (višek pri pribl. 580nm), (5) oranžna (višek pri pribl. 600nm), (6) rdeča (višek pri pribl. 650nm).

LS, Mann-Whitney U test, n=3, P<0.01). The level of inhibition was high throughout both experiments, although there were differences among colours in the violet-to-red test (Fig. 6d, SL, Kruskal-Wallis test, d.f.=7, P<0.01; LS, Kruskal-Wallis test, d.f.=7, P=NS). Fish tended to keep slightly stiller when longer-wavelength lights were presented first (SL vs LS, Mann-Whitney U test, n=3, P<0.01).

Overall, the peacock wrasse *S. tinca* L. was not particularly affected by monochromatic lights. Level of aggregation, attraction and inhibition were set on medium values and both within-and-between-experiment differences were either not pronounced or did not show a specific trend.

Both experiments had only a slight effect on levels of aggregation (Fig. 7a, SL, Kruskal-Wallis test, d.f.=7, P<0.01; LS, Kruskal-Wallis test, d.f.=7, P<0.05). Differences between experiments were not marked either (SL vs LS, Mann-Whitney U test, n=3, P=NS). Shifting colour from violet to red, fish were progressively more attracted at first (violet to green), then they tended to move farther from the light source (green to orange) and to get closer to it again in presence of red light (Fig. 7b,c, SL, Kruskal-Wallis test, d.f.=7, P<0.01). An inverse trend was detected during the red to violet experiment (Fig. 7b,c, LS, Kruskal-Wallis test, d.f.=7, P<0.01). The differences between the two experiments were significant, especially due to the higher attractive effect of green and yellow lights presented after the shorter-wavelength ones (SL vs LS, Mann-Whitney U test, n=3, P<0.01). The degree of inhibition was always medium-to-high, and the fluctuations were similar to those pointed out for the level of attraction (Fig. 7d, SL and LS, Kruskal-Wallis test, d.f.=7, P<0.01; SL vs LS, Mann-Whitney U test, n=3, P<0.01).

The white seabream *D. sargus* L. was characterised by low levels of aggregation and inhibition in presence of coloured lights, and it did not show any conspicuous phototactic response.

Levels of aggregation are low in all cases, although fish show a slightly higher cohesion in presence of short-to-medium wavelength lights (Fig. 8a, SL and LS, Kruskal-Wallis test, d.f.=7, P<0.01). There are no differences between the two experiments (SL vs LS, Mann-Whitney U test, n=3, P=NS). Fish were not particularly attracted by monochromatic lights, and there were not significant differences between colours either within and between experiments (Fig. 8b,c, SL and LS, Kruskal-Wallis test, d.f.=7, P=NS; LS vs SL, Mann-Whitney U test, n=3, P=NS). The level of inhibition was in general low, and the differences between colours were not significant when the colour was shifted from violet to red (Fig. 8d, SL, Kruskal-Wallis test, d.f.=7, P=NS). During the second experiment, inhibition was slightly higher in presence of yellow, green and blue lights (Fig. 8d, LS, Kruskal-Wallis test, d.f.=7, P<0.01). Between-experiment variations in the level of inhibition were not significant (LS vs SL, Mann-Whitney U test, n=3, P=NS).

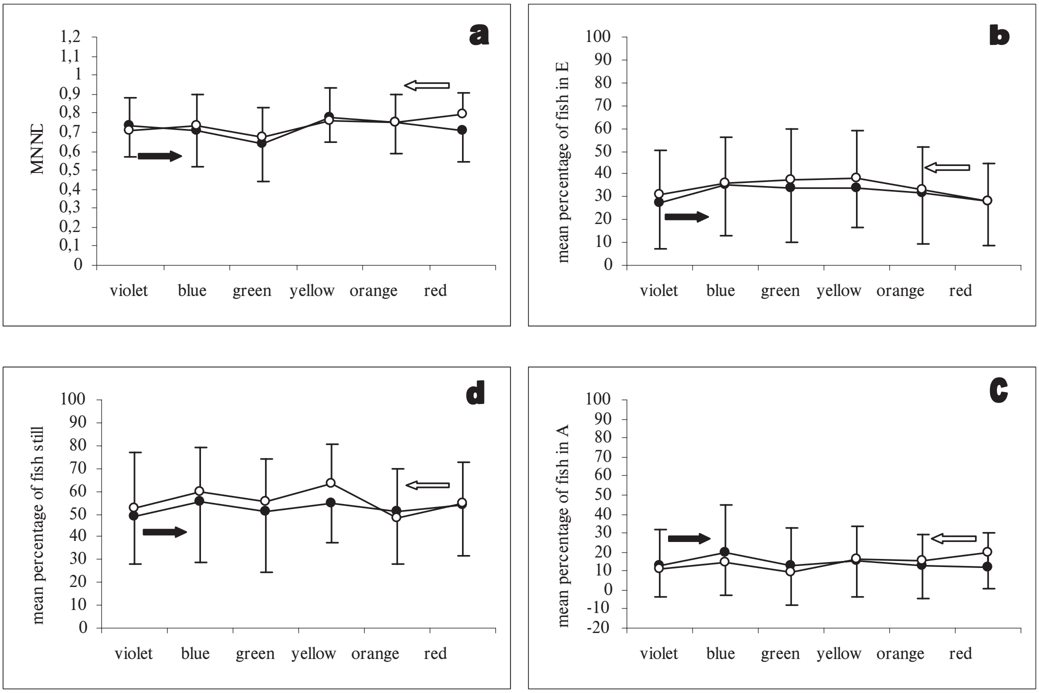

Figure 8: White seabream *D. sargus* L.
Effects of light colour variations on the following parameters: (a) mean nearest neighbour distance (MNND), (b) mean percentage of fish in the area closest to the light source (E), (c) mean percentage of fish in the area farther from the light source (A), (d) mean percentage of fish still. Filled circles and arrows indicate experiment SL: light colour progressively shifted from the Shorter (violet) to the Longer (red) wavelengths of the visual spectrum. Open circles and arrows indicate experiment LS: light colour progressively shifted from the Longer (red) to the Shorter (violet) wavelengths of the visual spectrum. Values given as means (n=3), bars ± one standard deviation. Colours tested: (1) violet (peak at approx. 410 nm), (2) blue (peak at approx. 460nm), (3) green (peak at approx. 525nm), (4) yellow (peak at approx. 580nm), (5) orange (peak at approx. 600nm), (6) red (peak at approx. 650nm).
Slika 8: Šarg D. sargus L.
Vplivi svetlobe različnih intenzitet na naslednje parametre: (a) srednja oddaljenost do najbližjih sosedov (MNND), (b) srednji odstotek rib v območju, najbližjem svetlobnemu viru (E), (c) srednji odstotek rib v območju, najbolj oddaljenem od svetlobnega vira (A), (d) srednji odstotek mirujočih rib. Polni krogci in puščice ponazarjajo eksperiment SL: svetla svetloba se je postopoma premikala od S (krajših – vijoličnih) do L (daljših – rdečih) valovnih dolžin vidnega spektra. Prazni krogci in puščice ponazarjajo eksperiment LS: svetla svetloba se je postopoma premikala od L (daljših – rdečih) do S (krajših-vijoličnih) valovnih dolžin vidnega spektra. Vrednosti, prikazane kot srednje (n=3), stolpci ± standardni odklon. Testirane barve: (1) vijolična (višek pri pribl. 410 nm), (2) modra (višek pri pribl. 460nm), (3) zelena (višek pri pribl. 525nm), (4) rumena (višek pri pribl. 580nm), (5) oranžna (višek pri pribl. 600nm), (6) rdeča (višek pri pribl. 650nm).

4. DISCUSSION

4.1 DEGREE OF REACTIVITY TO LIGHTS OF VARIABLE INTENSITY

Exposure to artificial lights of variable intensity had an effect on all species, although each of them reacted in a distinctive way. Behavioural responses were affected both by absolute illumination levels and by mode of intensity variation.

During both experiments, the brown meagre *S. umbra* L. was the most reactive to the presence of light. It was in all cases strongly disturbed by the presence of an illuminated field, in front of which it showed marked repulsion. The response was particularly pronounced when fish were exposed to high intensities first. On the contrary, the exposure to low-intensity lights at the beginning of the experiment induced a negative response at first (moving from crepuscular to diurnal conditions), but this was followed by a slight habituation to the increasing illumination levels.

The other three species were less influenced by light intensity variations. The peacock wrasse *S. tinca* L. showed the highest levels of aggregation and inhibition, together with a strong tendency to remain in proximity of the light source. However, the reactivity to variations in light conditions was not pronounced.

Blue damselfish *C. chromis* L. were in all cases rather dispersed along the tank and tended to keep still, probably due to their territorial habits. Phototactic reactions were not particularly marked, although fish tended to be attracted by strong lights, and to remain close to the light source even if the intensity was progressively decreased.

The white seabream *D. sargus* L. was the less influenced by variations in light intensity conditions. The group of fish tended to keep aggregated and moderately active throughout both experiments, and it was only slightly attracted by the presence of light. Positive phototactic reactions were more pronounced when light intensity was progressively decreased.

4.2 DEGREE OF REACTIVITY TO MONOCHROMATIC LIGHTS OF VARIABLE WAVELENGTH

Monochromatic lights of variable wavelength induced an effect on all species, although the reactions were different among them. Behavioural responses were affected both by quality and order of presentation of colours.

The brown meagre *S. umbra* L. showed the most dramatic reactions also when exposed to monochromatic lights. Repulsive reactions reached a peak with shorter-wavelength colours, such as violet, blue, and to a lesser extent green. Such colours induced a marked aggregation of the group of fish in the farthest and darkest corner of the tank, where they kept totally still. The behavioural response conforms to the narrow peak of absorbance 500-504 nm reported for the A1 visual pigment of members of the same family (Ali & Anctil, 1976).

The peacock wrasse *S. tinca* L. was less reactive to monochromatic stimuli. Aggregation and attraction to light were moderate, inhibition was medium-to-high. The only conspicuous differences between the two experiments were detected in the central bands of the visual spectrum. Indeed, fish were significantly more attracted by green and yellow lights when these were emitted after the shorter-wavelength ones, simulating the shift from crepuscular (prevalence of shorter wavelengths) to daylight (prevalence of longer wavelengths) conditions. Wider peaks of absorption and both A1 (484-527 nm) and A2 (510-513) visual pigments are reported for members of the same family (Ali & Anctil, 1976). Electrophysiological recordings of compound action potentials from retinal ganglion cells of *Thalassoma duperrey* Quoy & Gaimard evidence at least two sensitivity peaks for the on response at lambda (max) = 460 and 550 nm (Barry & Hawryshyn, 1999).

Similarly, the blue damselfish *C. chromis* L. was only slightly influenced by variations in light colours. Overall, the order of presentation of the different monochromatic lights did not affect markedly the behavioural responses of the group of fish. Aggregation was in all cases low and inhibition high, probably due to the territorial habits of the species. Phototactic responses were moderately positive independent of the colour, with the exception of red lights that induced a repulsive reaction. The family Pomacentridae is diurnal, planktivore and lives in visually complex habitats. A reported A1 visual pigment peak absorption of 491-497 nm along with the presence of A2 (Ali & Anctil, 1976) and a UV visual capability (Marshall & Vorobyev, 2003) accord with a broad range of spectral sensitivities and adaptation to an illuminated environment. Chromatic action spectra based on juvenile feeding behaviour response peak around lambda (max) 500 nm but shift to longer wavelengths occur during ontogeny (Job & Shand, 2001).

Among the four species, the white seabream *D. sargus* L. (A1 max 493-518 nm for the Sparidae: Ali & Anctil, 1976) showed the lowest reactions also in presence of monochromatic lights. Fish tended to keep moderately aggregated and active in all cases, and did not show any differential attraction to coloured lights that always induced a modest positive reaction.

4.3 ECOLOGICAL CHARACTERISATION OF VISUAL BEHAVIOUR AND OF PHOTOSENSITIVITY

Although some common evolutionary trends can be recognised in the adaptations to the underwater environment (e.g. Lythgoe, 1979), the visual behaviour of fish can vary conspicuously among species (Ben-Yami, 1976; Marchesan et al., 2003). Indeed, the visual behaviour of a species depends on both its biological features (e.g. morpho-physiology of the eye and visual system) and the ecological conditions of life (e.g. habitat, social structure, feeding habits) (Hobson et al., 1981; Helfman, 1993; Pankhurst & Hilder, 1998). Species characterised by different ecological requirements are therefore expected to show differences in their structural and behavioural adaptations to the presence of light, both in natural and artificial conditions. Conversely, we expect to draw an ecological classification of fish according to their behavioural reactions to light, as already suggested by Ben-Yami (1976).

In the present study, a very pronounced differentiation in the behavioural responses to light can be recognised between the brown meagre *S. umbra* L. and the other three species analysed. Indeed, the brown meagre is a strictly nocturnal species, thus adapted to very low light conditions and to the presence of a restricted band of wavelengths in the environment (mostly in the violet-blue range of the visual spectrum). This explains the strong sensitivity to both white and monochromatic lights, even at low intensities. Interestingly, the negative responses are particularly pronounced with violet and blue lights. This suggests that the brown meagre's eye and visual system – as supported by retina structure and visual pigment absorption peak (Ali & Anctil, 1976) – is finely tuned on such shorter wavelengths, in order to better move in a nocturnal environment. Indeed, such colours may be detected as very brilliant even at extremely low illumination levels, and for this reason they may have induced a repulsive reaction during the experiments described above.

The brown meagre *S. umbra* L. is a typical predator species, and its habits can be compared to those of tunas that live in deep sea (Ben-Yami, 1976). Repulsion for illuminated fields, associated to nocturnal and predatory habits, is reported also for other Sciaenidae living in coral reefs (Hobson, 1973). Furthermore, a preference for very low artificial light conditions has been highlighted in a number of predatory species, such as *Trachurus japonicus* Temminck & Schlegel and *Scomber japonicus* Houttuyn (Imamura & Takeuchi, 1960).

The other three species analysed show more similar responses to the presence of light. Overall, they are not particularly reactive to the exposure to different light conditions. However, a certain degree of differentiation can be recognized. The blue damselfish *C. chromis* L. is in an antithetic position compared to the brown meagre's one. Indeed, the blue damselfish is a strictly diurnal species, and it is therefore well adapted to strong light conditions and to the whole range of the visual spectrum, including UV. This explains why fish show a good tolerance to lights of variable intensity and wavelength throughout this study, maintaining their territorial habits independent of the illumination conditions. Interestingly, fish tend to perform some vertical movements when the light is progressively increased (pers. obs.), suggesting the presence of crepuscular vertical migrations in such a species, as described for other Pomacentridae (Hobson, 1973; Hobson et al., 1981).

The peacock wrasse *S. tinca* L. has also shown a good tolerance to differential light conditions throughout the study. This species, however, appears to be slightly more reactive to the presence of light of variable intensity and wavelength. In general, it is moderately attracted to white lights independent of their intensity, and to monochromatic lights in the central band of the visual spectrum (green-yellow). This is in accordance with its diurnal and crepuscular habits, and with its preferential habitats, as it can be found in vegetated coastal environments, where the underwater illumination is mainly centred in the green-yellow band of the spectrum.

The visual behaviour of blue damselfish and peacock wrasse can be compared to that of Pacific and Atlantic sauries (*Cololabis saira* Brevoort and *Scomberesox saurus* Walbaum) that show positive phototaxis and good tolerance to a wide variety of light intensities and colours (Ben-Yami, 1976). Blue damselfish, peacock wrasses and sauries are all diurnal species that live in coastal waters, characterised by high illumination most of the time, and that feed on plankton (blue damselfish, sauries) and on benthic preys (blue damselfish, peacock wrasse). Similar feeding habits and responses to light are highlighted also in coral reef Pomacentridae and Labridae (Hobson, 1973).

Among the three species, the white seabream *D. sargus* L. is the less influenced by light conditions, and it remains active even at low light intensities and with all type of monochromatic lights. This suggests that such a species is well adapted to a wider range of light intensities and colours. Indeed, the white seabream is active both during the day and at twilight, and to a certain extent it keeps feeding independent of the light conditions.

Although the white seabream *D. sargus* L. is not a typical predator, its visual behaviour is very similar to that of predatory fish such as *Scomber japonicus* Houttuyn, Carangidae and Thunidae (Ben-Yami, 1976). All these species are not particularly affected by the presence of light and they tend to keep active all the time, even if they often show a preference for medium-to-low light conditions. Considering the feeding habits of the white seabream, however, some similarities can be found with these predators. The white seabream is carnivorous, characterised by flexible circadian rhythms and it is active even at twilight (Sala & Ballesteros, 1997). A similar flexibility of circadian habits and feeding behaviour has been reported for *Gadus morhua* L. (Løkkeborg & Fernö, 1999).

5. SUMMARY

This study highlights that the behavioural reactions to lights of different intensity and wavelength can vary conspicuously among species, according to their visual traits and lifestyles. When conservation measures must be taken in order to avoid or at least attenuate underwater 'photopollution' inside marine protected areas (Witherington, 1997), the behaviour of the most photosensitive species should be taken into account. Species that would be strongly impacted by the presence of illuminated fields should be regarded as the limiting factor for the definition of the maximum level of illumination that could be tolerated without causing any disturbance on the fish community living inside a protected area.

POVZETEK

Pričujoča študija kaže, kako nenavadne so lahko vedenjske reakcije rib na svetlobo različne intenzitete in valovnih dolžin glede na vidne značilnosti in življenjski slog teh ribjih vrst. Kadar smo prisiljeni sprejeti naravovarstvene ukrepe, da bi se izognili ali pa vsaj omilili podvodno "svetlobno onesnaževanje" v zaščitenih morskih območjih (Witherington, 1997), moramo upoštevati vedenje vrste, ki je najbolj občutljiva za svetlobo. Vrste, ki jih osvetljena vodna polja najbolj prizadenejo, je treba jemati kot omejujoči dejavnik pri določanju največje dovoljene osvetljenosti, ki jo je še mogoče dopuščati, ne da bi s tem vznemirjali ribje skupnosti, živeče v zaščitenih morskih območjih.

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