

Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea

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Supplement. Additional Data

Table S1. Detailed species names of fish groups included in the Port-Cros MPA Ecopath model, a '+' indicating the presence of secondary species. Dusky grouper were split into 3 subgroups: small, medium and large. Small juveniles feed mainly on fish; medium adults, mainly on crabs and cephalopods; and large adults, mainly on cephalopods (Harmelin & Harmelin-Vivien 1999, Linde et al. 2004). Salema were separated into small individuals (<15 cm total length) and adults, as small salema feed mainly on shallow seaweeds, while adults also feed on *Posidonia oceanica* (Verlaque 1990)

Group name	Species name
Rays	<i>Raja</i> spp.
Dusky grouper	<i>Epinephelus marginatus</i>
Amberjack+	<i>Seriola dumerili</i> , <i>Conger conger</i> , <i>Lophius piscatorius</i> , <i>Dicentrarchus labrax</i> , <i>Muraena helena</i> , <i>Scyliorhinus canicula</i> , <i>Dentex dentex</i> , <i>Sphyrnaena viridensis</i>
Red scorpionfish+	<i>Phycis phycis</i> , <i>Labrus merula</i> , <i>Labrus viridis</i> , <i>Sciaena umbra</i> , <i>Scorpaena scrofa</i> , <i>Pagrus pagrus</i> , <i>Zeus faber</i>
Scorpionfishes+	<i>Scorpaena notata</i> , <i>Scorpaena porcus</i> , <i>Serranus cabrilla</i> , <i>Serranus hepatus</i> , <i>Serranus scriba</i> , <i>Synodus saurus</i>
Surmullet+	<i>Arnoglossus laterna</i> , <i>Bothus podas</i> , <i>Gaidropsarus mediterraneus</i> , <i>Gaidropsarus vulgaris</i> , <i>Trisopterus</i> spp., <i>Mullus surmuletus</i> , <i>Ophisurus serpens</i> , <i>Ophidion rochei</i> , <i>Parophidion vassali</i>
Pipefishes+	<i>Apogon imberbis</i> , <i>Apletodon dentatus</i> , <i>Diplecogaster bimaculata</i> , <i>Lepadogaster candolei</i> , <i>Opeatogenys gracilis</i> , <i>Hippocampus</i> spp., <i>Nerophis maculatus</i> , <i>Syngnathus acus</i> , <i>Syngnathus typhle</i> , <i>Tripterygion</i> spp.
Wrasses	<i>Coris julis</i> , <i>Symphodus cinereus</i> , <i>Symphodus doderleini</i> , <i>Symphodus mediterraneus</i> , <i>Symphodus melanocercus</i> , <i>Symphodus ocellatus</i> , <i>Symphodus roissali</i> , <i>Symphodus rostratus</i> , <i>Symphodus tinca</i> , <i>Thalassoma pavo</i>
Gobies	<i>Deltentosteus colonianus</i> , <i>Deltentosteus quadrimaculatus</i> , <i>Gobius auratus</i> , <i>Gobius cruentatus</i> , <i>Gobius fallax</i> , <i>Gobius geniporus</i> , <i>Gobius paganellus</i> , <i>Gobius vittatus</i> , <i>Pomatoschistus minutus</i> , <i>Pomatoschistus quagga</i> , <i>Thorogobius ephippiatus</i> , <i>Thorogobius macrolepis</i>
Pagellus	<i>Pagellus</i> spp.
Diplodus+	<i>Diplodus puntazzo</i> , <i>Diplodus sargus</i> , <i>Diplodus vulgaris</i> , <i>Lithognathus mormyrus</i> , <i>Sparus aurata</i> , <i>Spondyliosoma cantharus</i>
Blennies+	<i>Blennius ocellaris</i> , <i>Diplodus annularis</i> , <i>Parablennius gattorugine</i> , <i>Parablennius rouxi</i>
Horse mackerels+	<i>Atherina</i> spp., <i>Trachurus</i> spp., <i>Spicara maena</i> , <i>Spicara smaris</i> , <i>Chromis chromis</i> , <i>Anthias anthias</i> , <i>Boops boops</i> , <i>Oblada melanura</i>
Mullet	<i>Mugilidae</i>
Salema	<i>Sarpa salpa</i>

Table S2. Input data and references by species for the fish groups in the Port-Cros MPA Ecopath model. Parameters are: landings (Y , $t\ km^{-2}\ yr^{-1}$) (from Cadiou & Bonhomme 2006), biomass in habitat area (b , $t\ km^{-2}\ yr^{-1}$), types of habitat (T: total area of the Port-Cros MPA; H: hard bottoms; S: soft bottoms; P: Posidonia beds), % of habitat—percentage of the surface of the Port-Cros MPA area occupied by the type of habitat designed [each species was assigned habitat preferences among hard bottoms (shallow rocky bottoms and deep rocky bottoms called coralligenous bottoms), soft bottoms (sandy and muddy bottoms), and seagrass meadows (mainly Posidonia beds)] (from Belsher et al. 2005), biomass in the total area of the Port-Cros MPA (B , $t\ km^{-2}\ yr^{-1}$), with maximal biomass values in each group in **bold**. Biomasses of ontogenic groups (dusky grouper and salema) were recalculated by Ecopath, as the stages are linked in the model, and their respective B , Q/B , and growth values are calculated from a baseline estimate for adults. Detailed references by species (ref.) are given for the biomass b and for the diet compositions DC (see references list)

Group name	Species name	Y	b	b ref.	Habitat		B	DC ref.
					Type	%		
Rays	<i>Raja spp.</i>	0.003	-	-	-	-	-	29
Dusky grouper	<i>Epinephelus marginatus</i>	-	4.994	17	T	100%	4.994	19, 25
Amberjack +	<i>Seriola dumerili</i>	0.002	2.700	18	T	100%	2.700	1
	<i>Conger conger</i>	0.010	0.116	13, 24, 31	H	7%	0.008	24
	<i>Lophius piscatorius</i>	0.003	0.300	10	S+H	70%	0.210	15
	<i>Dicentrarchus labrax</i>		0.580	11	H+P	37%	0.215	8
	<i>Muraena helena</i>	0.010	4.096	13, 35	H	7%	0.287	15
	<i>Scyliorhinus canicula</i>		0.017	24	H+P	37%	0.006	27
	<i>Dentex dentex</i>	0.004	5.426	13, 35	H+P	37%	2.008	28
	<i>Sphyræna viridensis</i>		0.116	10	T	100%	0.116	2
Red scorpionfish +	<i>Phycis phycis</i>	0.014	0.060	13	H	7%	0.004	39
	<i>Labrus merula</i>	0.012	0.237	12, 13, 24	H+P	37%	0.088	3
	<i>Labrus viridis</i>							24
	<i>Sciaena umbra</i>	0.002	0.604	18, 21	H	7%	0.042	39
	<i>Scorpaena scrofa</i>	0.047	4.033	13, 24, 35	H	7%	0.282	24
	<i>Pagrus pagrus</i>	0.002	0.080	13	H+P	37%	0.030	7
	<i>Zeus faber</i>	0.002	0.045	10	T	100%	0.045	3
Scorpionfishes +	<i>Scorpaena notata</i>	0.012	6.552	24, 35	H+P	37%	2.424	24
	<i>Scorpaena porcus</i>							0.954
	<i>Serranus cabrilla</i>		3.829	12, 13, 24, 35	H+P	37%	1.417	24
	<i>Serranus hepatus</i>	0.019	0.003	24	S	63%	0.002	3
	<i>Serranus scriba</i>							0.193
	<i>Synodus saurus</i>		0.041	24	S	63%	0.026	24
Surmullet +	<i>Arnoglossus laterna</i>		0.001	24	S	63%	0.001	24
	<i>Bothus podas</i>		0.015	24	S	63%	0.010	24
	<i>Gaidropsarus mediterraneus</i>		0.058	24	H	7%	0.004	24
	<i>Gaidropsarus vulgaris</i>		0.075	24	H	7%	0.005	24
	<i>Trisopterus spp.</i>		0.014	13	H	7%	0.001	16, 30
	<i>Mullus surmuletus</i>	0.030	0.185	13, 24, 31	S	63%	0.117	24
	<i>Ophisurus serpens</i>		0.100	10	S	63%	0.063	-
	<i>Ophidion rochei</i>		0.002	24	S	63%	0.002	24
	<i>Parophidion vassali</i>		0.053	24	S	63%	0.033	24
Pipefishes +	<i>Apogon imberbis</i>		0.033	13, 35	H	7%	0.002	39
	<i>Apletodon dentatus</i>		0.001	24	H+P	37%	0.005	24
	<i>Diplecogaster bimaculata</i>		0.000	24	H+P	37%	0.000	24
	<i>Lepadogaster candolei</i>		0.004	24	H+P	37%	0.001	24
	<i>Opeatogenys gracilis</i>		0.000	24	P	30%	0.000	24
	<i>Hippocampus spp.</i>		0.006	24	P	30%	0.002	24
	<i>Nerophis maculatus</i>		0.006	24	P	30%	0.002	24
	<i>Syngnathus acus</i>		0.030	24	P	30%	0.009	24
	<i>Syngnathus typhle</i>		0.008	24	P	30%	0.002	24
	<i>Tripterygion spp.</i>		0.024	13, 24	H	7%	0.002	24
Wrasses	<i>Coris julis</i>		4.336	12, 13, 24, 35	T	100%	4.336	24
	<i>Symphodus cinereus</i>		0.044	12, 24	S	63%	0.028	24
	<i>Symphodus doderleini</i>		0.003	13, 24	H+P	37%	0.001	24
	<i>Symphodus mediterraneus</i>	0.019	0.094	12, 13, 24, 35	H+P	37%	0.035	24
	<i>Symphodus melanocercus</i>		0.038	12, 13, 24	H+P	37%	0.014	24
	<i>Symphodus ocellatus</i>		0.383	12, 13, 24	H+P	37%	0.142	24

	<i>Symphodus roissali</i>		0.009	12, 13, 24	H+P	37%	0.003	24
	<i>Symphodus rostratus</i>		0.084	12, 13, 24	H+P	37%	0.031	24
	<i>Symphodus tinca</i>		1.091	12, 13, 24	H+P	37%	0.404	24
	<i>Thalassoma pavo</i>		0.124	22	H+P	37%	0.046	9
Gobies	<i>Deltentosteus colonianus</i>		0.022	24	T	100%	0.022	24
	<i>Deltentosteus quadrimaculatus</i>		0.000	24	T	100%	0.000	3
	<i>Gobius auratus</i>		0.113	13	T	100%	0.113	39
	<i>Gobius cruentatus</i>		0.013	24	T	100%	0.013	24
	<i>Gobius fallax</i>		0.013	24	T	100%	0.013	24
	<i>Gobius geniporus</i>		0.033	24	T	100%	0.033	24
	<i>Gobius paganellus</i>		0.024	24	T	100%	0.024	24
	<i>Gobius vittatus</i>		0.146	13	T	100%	0.146	24
	<i>Pomatoschistus minutus</i>		0.002	24	T	100%	0.002	24
	<i>Pomatoschistus quagga</i>		0.000	24	T	100%	0.000	24
	<i>Thorogobius ephippiatus</i>		0.055	35	T	100%	0.055	15
	<i>Thorogobius macrolepis</i>		0.007	13	T	100%	0.007	-
Pagellus	<i>Pagellus spp.</i>	0.003	-	-	-	-	-	34
Diplodus +	<i>Diplodus puntazzo</i>		4.622	13, 35	H+P	37%	1.710	37
	<i>Diplodus sargus</i>	0.021	2.208	13	H+P	37%	0.817	37
	<i>Diplodus vulgaris</i>		0.054	13	H+P	37%	0.020	3
	<i>Lithognathus mormyrus</i>		0.030	10	S	63%	0.019	23
	<i>Sparus aurata</i>	0.001	1.602	11, 13, 35	S	63%	1.009	3
	<i>Spondylisoma cantharus</i>	0.007	0.053	12, 13, 24	T	100%	0.053	24
Blennies +	<i>Blennius ocellaris</i>							24
	<i>Parablennius gattorugine</i>		0.120	13, 24, 35	H+P	37%	0.044	24
	<i>Parablennius rouxi</i>							39
	<i>Diplodus annularis</i>		0.282	12, 13, 24	H+P	37%	0.104	24
Horse mackerels +	<i>Atherina spp.</i>		75.000	10	H+P	37%	27.750	24
	<i>Trachurus spp.</i>		75.000	10	H+P	37%	27.750	38
	<i>Spicara maena</i>							24
	<i>Spicara smaris</i>		0.565	13, 24, 35	H+P	37%	0.209	24
	<i>Chromis chromis</i>		0.951	13, 24	H+P	37%	0.352	24
	<i>Anthias anthias</i>		24.988	13, 35	H	7%	1.749	15
	<i>Boops boops</i>	0.012	0.034	13	H+P	37%	0.012	3
	<i>Oblada melanura</i>		0.747	18	H+P	37%	0.276	39
Mulletts	Mugilidae		4.502	10, 13	T	100%	4.502	4
Salema	<i>Sarpa salpa</i>	-	9.500	12	H+P	37%	9.500	42

Table S3. Input data and references for the other (non-fish) groups in the Port-Cros MPA Ecopath model. Parameters are biomass in habitat area (b , $t\ km^{-2}\ yr^{-1}$), dry weight (DW), wet weight (WW), dry to wet weight conversion ratio (WW/DW), types of habitat (T: total area of the Port-Cros MPA; H: hard bottoms; H deep: deep hard bottoms; S: soft bottoms; P: Posidonia beds), % of habitat—percentage of the surface of the Port-Cros MPA area occupied by the type of habitat designed [each species was assigned habitat preferences among hard bottoms (shallow rocky bottoms and deep rocky bottoms called coralligenous bottoms), soft bottoms (sandy and muddy bottoms), and seagrass meadows (mainly Posidonia beds)] (from Belsher et al. 2005), biomass in the total area of the Port-Cros MPA (B , $t\ km^{-2}\ yr^{-1}$), production/biomass (P/B , yr^{-1}), and consumption/biomass (Q/B , yr^{-1}). Detailed references (ref.) are given for the biomass b in DW, the P/B and the Q/B ratios (see references list)

Group name	b DW	b ref.	WW/DW	b WW	Habitat Type	Habitat %	B	Studied species for biomass data	P/B ref.	Q/B ref.
Seabirds	-	5	-	-	-	-	0.290	<i>Calonectris diomedea</i> , <i>Larus michahellis</i> , <i>Puffinus yelkouan</i>	36	6 ^a
Cephalopods	-	10	-	1	T	100%	1	<i>Octopus vulgaris</i>	6 ^a	-
Crabs	2.5	41	3.9	9.75	H+P	37%	3.608	<i>Achaeus cranchii</i> , <i>Eurynome spinosa</i> , other Brachyura	32 ^a	32
Decapods	-	-	-	-	-	-	-	-	32 ^a	-
Bivalves	-	10	-	1	P+S	93%	0.930	<i>Pinna nobilis</i>	32 ^a	32 ^a
Gastropods	-	-	-	-	-	-	-	-	33	33
Sea stars	0.2	11	3.5	0.7	T	100%	0.700	<i>Marthasterias glacialis</i>	11	-
Brittle stars +	-	-	-	-	-	-	-	-	32 ^a	32 ^a
Sea urchins	33.3	11	3.1	103.23	H+P	37%	38.195	<i>Psammechinus microtuberculatus</i> , <i>Paracentrotus lividus</i>	11	-
Sea cucumbers	7.55	11	10.1	76.255	T	100%	76.255	<i>Holothuria tubulosa</i> & <i>Holothuria polii</i>	11	11
Sea worms	-	-	-	-	-	-	-	-	6 ^a	6 ^a
Supensivores	-	-	-	-	-	-	-	-	32 ^a	32 ^a
Gorgonians	257.5	20	4.5	1158.75	H deep	3.5%	40.556	<i>Paramuricea clavata</i>	32 ^a	-
Small crustaceans	4.5	11	6.9	31.05	T	100%	31.050	-	11	32 ^a
Amphipods	-	-	-	-	-	-	-	-	11	-
Large zooplankton	-	-	-	-	-	-	-	-	33	-
Small zooplankton	-	-	-	-	-	-	-	-	33	33
Forams	-	-	-	-	-	-	-	-	32, 33	-
Seagrass	5000	11	5.7	28500	P	30%	8550	<i>Posidonia oceanica</i>	11	-
Shallow seaweeds	774.5	14	5.2	4027.4	H sha,	3.5%	140.959	Chlorophyceae, Phaeophyceae, Rhodophyceae, other algae	26	-
Deep seaweeds	225	40	5.2	1170	H deep	3.5%	40.950	<i>Cystoseira balearica</i> , other cystoseires	33 ^a	-
Phytoplankton	-	-	-	-	-	-	14 ^b	-	33	-
Detritus	-	-	-	-	-	-	86.354 ^c	-	-	-

^aSynthesis of different values cited in the reference

^bCalculated from the value of primary production in the western Mediterranean Sea: $175\ g\ C\ m^{-2}\ yr^{-1}$ (Chassot et al. 2007)

^cEstimated with an empirical equation (Christensen & Pauly 1993), using a value of 25 m for the euphotic zone depth in the MPA

References list for tables S2 & S3:

1: Badalamenti et al. (1995); 2: Barreiros et al. (2002); 3: Bell & Harmelin-Vivien (1983); 4: Blanco et al. (2003); 5: calculated from counts of nesting couples realized in Port-Cros islands from 2004 to 2007 and accounting on the time they spent inside the reserve (K Bourgeois, pers. comm.); 6: Coll et al. (2006); 7: Chakroun-Markouz & Kartas (1987); 8: Costa (1988); 9: Donner & Herrer (2004); 10: Francour (pers. comm.); 11: Francour (1990); 12: Francour (1997); 13: Francour (2007); 14: Frantzis et al. (1988); 15: Froese & Pauly (2009); 16: Gramitto (1999); 17: Harmelin (pers. comm.); 18: JG Harmelin (1987); 19: Harmelin & Harmelin-Vivien (1999); 20: Harmelin & Garrabou (2005); 21: Harmelin & Ruitton (2007); 22: Hereu (2004); 23: Kallianotis et al. (2005); 24: Khoury (1987); 25: Linde et al. (2004); 26: Mackinson (1999); 27: Macpherson (1981); 28: Morales-Nin & Moranta (1997); 29: Morato et al. (2003); 30: Morte et al. (2001); 31: Ody (1987); 32: Opitz (1996); 33: Pinnegar (2000); 34: Rosecchi (1993); 35: Ruitton et al. (2004); 36: Russell et al. (1999); 37: Sala & Ballesteros (1997); 38: Santic et al. (2003); 39: Stergiou & Karpouzi (2002); 40: T Thibault (pers. comm.); 41: Vadon (1981); 42: Verlaque (1990)

Table S4. Diet composition table of the Ecopath model of the Port-Cros MPA. Groups displayed in columns are considered as predator groups, feeding on the groups displayed in rows, considered as their prey. The proportion of each prey group in the predator's diet is indicated by the displayed values. Blank cells are zero values, indicating that the predator does not feed on this prey in the model. Import represent food sources coming from outside the ecosystem. Total should be one for all predator groups as it is the sum of the proportions of all prey groups in the diet of each predator group

Group name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
1 Seabirds																			
2 Rays																			
3 Dusky grouper— large																			
4 Dusky grouper— medium						0.010													
5 Dusky grouper— small																			
6 Amberjack+				0.022	0.041														
7 Red scorpionfish+				0.022	0.041														
8 Scorpionfishes+				0.030	0.041	0.117	0.035												
9 Surmullet+		0.290		0.009	0.031	0.037	0.004												
10 Pipefishes+				0.002	0.016	0.007													
11 Wrasses				0.017	0.031	0.087	0.173												
12 Gobies				0.017	0.031	0.067	0.017		0.001										
13 Pagellus		0.290				0.018													
14 Diplodus+				0.032	0.031	0.112	0.035												
15 Blennies+				0.009	0.031	0.037													
16 Horse mackerels+	0.004			0.022	0.034	0.121	0.246	0.678	0.227										
17 Mulletts						0.015	0.002												

Table S5. Methods used to estimate the natural mortality rate (M , yr^{-1}) and the consumption/biomass ratio (Q/B , yr^{-1}) by fish species for the Port-Cros marine protected area Ecopath model. Parameters are maximal age (t_{\max} , yr), Von Bertalanffy growth parameter (K , yr^{-1}), length at infinity (L_{inf} , cm), weight at infinity (W_{inf} , g), aspect ratio of the tail (A , dimensionless). Values of all these parameters were taken from FishBase (Froese & Pauly 2009). Empirical equations used to calculate M : $M = \exp[1.46 - 1.01 \times \text{Ln}(t_{\max})]$ (Hoenig 1993); $M = \exp[-0.0152 - 0.279 \times \text{Ln}(L_{\text{inf}}) + 0.6543 \times \text{Ln}(K) + 0.463 \times \text{Ln}(T)]$ with $T = 19^\circ\text{C}$ (Pauly 1980); $M = 1.89 \times K$ (Gascuel et al. 2008). Empirical equation used to calculate Q/B : $\log_{10}(Q/B) = 7.964 - 0.204 \times \log_{10}(W_{\text{inf}}) - 1.965 \times T + 0.083 \times A + 0.532 \times h + 0.398 \times d$ (Palomares & Pauly 1998) with $T = 1000 / (T + 273.15)$ and $T = 19^\circ\text{C}$, h and d are constants defined by the diet type

Group name	Species name	t_{\max}	K	L_{inf}	Natural mortality rate M				W_{inf}	A	Q/B
					Hoenig	Pauly	Gascuel	Average			
Rays	<i>Raja</i> spp.	23	0.10	117	0.18	0.23	0.19	0.20	12520	0.00	2.52
Dusky grouper	<i>Epinephelus marginatus</i>	50	0.08	136	–	–	–	–	40161	1.48	2.64
Amberjack+	<i>Seriola dumerili</i>	15	0.19	175	0.28	0.31	0.36	0.32	62009	3.01	3.24
	<i>Conger conger</i>	19	0.06	265	0.22	0.13	0.12	0.16	35505	0.00	2.04
	<i>Lophius piscatorius</i>	24	0.11	132	0.17	0.23	0.21	0.20	28195	–	–
	<i>Dicentrarchus labrax</i>	15	0.19	83	0.28	0.38	0.36	0.34	6529	1.22	3.64
	<i>Muraena helena</i>	–	–	153	–	–	–	–	–	–	–
	<i>Scyliorhinus canicula</i>	12	0.12	87	0.35	0.28	0.23	0.28	2683	–	–
	<i>Dentex dentex</i>	–	0.08	95	–	0.21	0.15	0.18	10599	1.83	3.70
	<i>Sphyraena viridensis</i>	–	0.09	101	–	0.22	0.17	0.20	3971	1.48	4.23
Red scorpionfish+	<i>Phycis phycis</i>	–	–	67	–	–	–	–	4348	1.37	4.07
	<i>Labrus merula</i>	17	0.22	44	0.25	0.50	0.42	0.39	1462	0.82	4.58
	<i>Labrus viridis</i>	18	–	55	0.23	–	–	0.23	–	1.15	–
	<i>Sciaena umbra</i>	13	0.22	47	0.32	0.49	0.42	0.41	4369	1.76	4.38
	<i>Scorpaena scrofa</i>	8	–	52	–	–	–	–	2366	1.49	4.71
	<i>Pagrus pagrus</i>	18	0.14	65	0.23	0.33	0.26	0.28	4165	2.02	4.65
	<i>Zeus faber</i>	12	0.29	60	0.35	0.55	0.55	0.48	3518	1.68	4.51
Scorpionfishes+	<i>Scorpaena notata</i>	–	–	–	–	–	–	–	286	1.34	7.05
	<i>Scorpaena porcus</i>	6	0.16	29	0.70	0.45	0.30	0.49	447	1.36	6.46
	<i>Serranus cabrilla</i>	8	0.38	32	0.53	0.78	0.72	0.67	103	1.18	8.42
	<i>Serranus hepatus</i>	–	0.36	15	–	0.92	0.68	0.80	62	2.23	11.40
	<i>Serranus scriba</i>	12	0.19	30	0.35	0.50	0.36	0.40	349	1.28	6.69
	<i>Synodus saurus</i>	–	–	–	–	–	–	–	937	2.85	7.39
Surmullet+	<i>Arnoglossus laterna</i>	8	–	16	0.53	–	–	0.53	–	0.77	–
	<i>Bothus podas</i>	–	–	17	–	–	–	–	1357	1.23	5.02
	<i>Gaidropsarus mediterraneus</i>	–	0.60	27	–	1.10	1.13	1.12	81	0.90	8.38
	<i>Gaidropsarus vulgaris</i>	6	–	–	0.70	–	–	0.70	2787	0.99	4.14
	<i>Trisopterus</i> spp.	4	0.21	46	1.06	0.48	0.40	0.65	741	0.88	5.32
	<i>Mullus surmuletus</i>	10	0.30	28	0.42	0.69	0.57	0.56	304	1.38	7.01
	<i>Ophisurus serpens</i>	–	–	–	–	–	–	–	3536	0.00	3.27
	<i>Ophidion rochei</i>	–	–	–	–	–	–	–	132	0.00	6.38
	<i>Parophidion vassal</i>	–	–	–	–	–	–	–	–	0.00	–
Pipefishes+	<i>Apogon imberbis</i>	–	0.90	15	–	1.69	1.70	1.69	56	1.39	9.92

	<i>Apletodon dentatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Diplecogaster bimaculata</i>	-	-	-	-	-	-	-	-	0.40	-
	<i>Lepadogaster candolei</i>	-	-	-	-	-	-	-	-	-	-
	<i>Opeatogenys gracilis</i>	-	-	-	-	-	-	-	-	-	-
	<i>Hippocampus</i> spp.	-	-	-	-	-	-	-	6	-	-
	<i>Nerophis maculatus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Syngnathus acus</i>	-	-	-	-	-	-	-	113	-	-
	<i>Syngnathus typhle</i>	-	0.56	26	-	1.06	1.06	1.06	6	-	-
Wrasses	<i>Tripterygion</i> spp.	-	-	-	-	-	-	-	-	-	-
	<i>Coris julis</i>	8	0.11	27	0.53	0.36	0.21	0.37	154	1.61	8.42
	<i>Symphodus cinereus</i>	6	-	-	-	-	-	-	-	1.53	-
	<i>Symphodus doderleini</i>	-	-	-	-	-	-	-	-	1.20	-
	<i>Symphodus mediterraneus</i>	8	-	-	-	-	-	-	-	1.19	-
	<i>Symphodus melanocercus</i>	-	-	-	-	-	-	-	59	1.09	9.27
	<i>Symphodus ocellatus</i>	5	-	-	-	-	-	-	-	1.13	-
	<i>Symphodus roissali</i>	8	0.35	15	0.53	0.91	0.66	0.70	62	1.05	9.10
	<i>Symphodus rostratus</i>	4	-	-	-	-	-	-	-	1.19	-
	<i>Symphodus tinca</i>	10	0.25	28	0.43	0.61	0.47	0.50	439	1.65	6.85
Gobies	<i>Thalassoma pavo</i>	-	-	-	-	-	-	-	-	1.05	-
	<i>Deltentosteus colonianus</i>	-	-	-	-	-	-	-	-	-	-
	<i>Deltentosteus quadrimaculatus</i>	-	-	-	-	-	-	-	5	0.75	14.28
	<i>Gobius auratus</i>	-	-	-	-	-	-	-	-	0.66	-
	<i>Gobius cruentatus</i>	-	-	-	-	-	-	-	84	0.69	8.00
	<i>Gobius fallax</i>	-	-	-	-	-	-	-	8	0.67	12.79
	<i>Gobius geniporus</i>	-	-	-	-	-	-	-	-	0.43	-
	<i>Gobius paganellus</i>	10	0.73	14	0.42	1.51	1.38	1.10	36	0.78	9.67
	<i>Gobius vittatus</i>	-	-	-	-	-	-	-	-	0.41	-
	<i>Pomatoschistus minutus</i>	3	0.93	9	1.42	1.98	1.76	1.72	11	1.07	13.00
	<i>Pomatoschistus quagga</i>	-	-	-	-	-	-	-	-	0.90	-
	<i>Thorogobius ephippiatus</i>	9	0.23	14	0.47	0.71	0.43	0.54	-	0.48	-
	<i>Thorogobius macrolepis</i>	-	-	-	-	-	-	-	-	1.23	-
Pagellus	<i>Pagellus</i> spp.	20	0.24	31	0.21	0.58	0.45	0.41	608	2.60	7.69
Diplodus+	<i>Diplodus puntazzo</i>	8	0.36	62	0.53	0.62	0.68	0.61	14101	3.10	4.46
	<i>Diplodus sargus</i>	10	0.12	47	0.42	0.33	0.23	0.33	1585	3.24	7.15
	<i>Diplodus vulgaris</i>	9	0.39	29	0.47	0.81	0.74	0.67	573	4.72	11.67
	<i>Lithognathus</i>	12	0.28	33	0.35	0.63	0.53	0.50	425	2.87	8.71

	<i>mormyrus</i>										
	<i>Sparus aurata</i>	11	0.27	58	0.38	0.53	0.51	0.47	2497	1.39	4.57
	<i>SpondylIOSoma</i>										
	<i>cantharus</i>										
Blennies+	<i>Blennius ocellaris</i>	–	–	21	–	–	–	–	120	1.19	8.18
	<i>Parablennius</i>										
	<i>gattorugine</i>	–	–	32	–	–	–	–	600	0.92	5.59
	<i>Parablennius</i>										
	<i>rouxi</i>	–	–	9	–	–	–	–	–	–	–
	<i>Diplodus</i>										
	<i>annularis</i>	7	0.27	25	0.60	0.67	0.51	0.59	286	1.58	7.38
Horse	<i>Atherina</i> spp.	4	0.26	11	1.06	0.83	0.49	0.79	15	1.20	12.60
mackerels+	<i>Trachurus</i> spp.	12	0.23	39	0.35	0.53	0.43	0.44	552	1.69	6.59
	<i>Spicara maena</i>	5	0.18	18	0.85	0.56	0.34	0.58	215	3.12	10.50
	<i>Spicara smaris</i>	7	0.19	20	0.60	0.56	0.36	0.51	192	2.86	10.23
	<i>Chromis chromis</i>	–	0.25	15	–	0.74	0.47	0.60	40	1.13	10.13
	<i>Anthias anthias</i>	–	–	–	–	–	–	–	399	2.16	7.70
	<i>Boops boops</i>	6	0.18	32	0.70	0.48	0.34	0.51	217	0.97	6.95
	<i>Oblada melanura</i>	11	0.23	33	0.38	0.55	0.43	0.46	489	2.48	7.86
Mulletts	Mugilidae	16	0.29	59	0.26	0.55	0.55	0.45	976	2.53	17.23
Salema	<i>Sarpa salpa</i>	11	0.23	45	–	–	–	–	1282	2.85	23.58

Balancing the Ecopath model

Balancing the model required the modification of some input values in 3 steps. First, we had to adjust some input consumption/biomass (Q/B) parameters that seemed to be unrealistically high. This was especially the case for some fish groups (wrasses, gobies, and blennies) for which no values of length at infinity (L_{inf}) were available for most species. For these groups, production/biomass (P/Q) was fixed and Q/B was estimated by the model (Table 1).

Then, although data on fish diet compositions were considered reliable, as diets were collected for every species in each group, some adjustments were necessary. For instance, stomach contents analysis of rays, carried out in the Azores Islands (Morato et al. 2003), was readjusted by removing pelagic fishes. Also, predation by the abundant amberjack+ group (fish groups were named using the most abundant species of the group, a '+' indicating the presence of secondary species) on decapods, gastropods, sea worms, and suspensivores had to be reduced. Indeed, the overly high fish consumption on these invertebrate groups led to overestimated biomass and, consequently, to insufficient primary production in the ecosystem. Data on the compositions of invertebrates' diet were less reliable. For example, the sea cucumbers' diet, from a stomach contents analysis realized in the Port-Cros MPA (Berthon 1987), initially included plants, which were replaced by detritus, based on the field knowledge that these species are detritivorous and not grazers. Cannibalism was reduced to the minimum values in diet compositions of decapod, gastropod, and sea worm groups, because the biomass estimated by the model appeared to be artificially increased by the high proportion of cannibalism in their original diets. Diets taken from other regions, and notably the Bay of Revellata on Corsica (Pinnegar 2000), did not mention salema, mullets, posidonia, or deep seaweeds, which were added to the diets of some groups. For instance, we transferred predation by crustaceans (decapods, small crustaceans, and amphipods) and by gastropods from seaweeds to *Posidonia oceanica*. Predation on some of the low biomass groups (e.g. surmullet+, blennies+, gobies, and pipefishes+) was reduced and transferred to similar groups with higher biomass.

Finally, biomass estimates were corrected for 3 groups. Biomass of cephalopods and bivalves had to be increased to sustain predation. Indeed, the biomass of these 2 groups was based on underestimated abundance values of only 1 species of each group (respectively, *Octopus vulgaris* and *Pinna nobilis*). Although these 2 species were the most abundant in the groups, we assumed that each biomass value could be tripled. Finally, biomass of horse mackerels+ was decreased 3-fold as the initial value, as biomass estimates for *Trachurus* spp. and *Atherina* spp. seemed too high (P. Francour pers. obs.). We also had to include 40% of imported prey in their diet, assuming frequent movements outside the reserve. Both steps

allowed us to balance the model and to relieve pressure on lower trophic level prey (large and small zooplankton and phytoplankton).

The EcoTroph model: principles and major equations

In the EcoTroph approach, the trophic ecosystem functioning is modeled as a continuous flow of biomass surging up the food web, from lower to higher trophic levels, because of predation and ontogenic processes. Thus, according to the usual equations of fluid dynamics, the flow of the biomass present in the ecosystem at trophic level τ under steady-state conditions is equal to:

$$\Phi(\tau) = D(\tau) \times K(\tau) \quad (S1)$$

where $\Phi(\tau)$ refers to the amount of biomass that moves up the food web through trophic levels τ (expressed in $t \text{ yr}^{-1}$), $D(\tau)$ is the density of biomass at trophic level τ (defined as the derivative of biomass with respect to trophic level τ and expressed in $t \text{ TL}^{-1}$, t being tons and TL being the trophic level), and $K(\tau)$ is the speed of the flow (in $\text{TL} \text{ yr}^{-1}$, i.e. the number of trophic levels crossed per year), which quantifies the velocity of biomass transfers through the food web.

The continuous distribution of the biomass across a trophic level is calculated using a discrete approximation based on small trophic classes. Conventionally, EcoTroph considers trophic classes of width $\Delta\tau$ equal to 0.1 TL , from Trophic Level 2 (corresponding to first-order consumers) to Trophic Level 5 (value being considered sufficient to cover all top predators likely to occur in marine ecosystems). Thus, the mean biomass $B\tau$ (in t), which is present in the $(\tau, \tau + \Delta\tau)$ trophic class under steady-state conditions, can be estimated as $\int D(\tau) \times d\tau$ or $D(\tau) \times \Delta\tau$ for a small interval $\Delta\tau$. Therefore:

$$B\tau = \Phi\tau \times \Delta\tau / K\tau \quad (S2)$$

where $\Phi\tau$ and $K\tau$ are the mean biomass flow and mean speed of flow within the $(\tau, \tau + \Delta\tau)$ trophic class, respectively.

The biomass flow decreases from low to high trophic levels because of catches and natural losses occurring during trophic transfers (due to non-predation mortalities, respiration and excretion). This leads to the following equation of the biomass flow:

$$\Phi(\tau, \tau + \Delta\tau) = \Phi(\tau) \times \exp[-(\mu\tau + \varphi\tau) \times \Delta\tau] \quad (S3)$$

where $\mu\tau$ is the net natural loss rate of biomass flow and $\varphi\tau$ is the loss rate due to fishing, per trophic class.

The speed of the flow has to be determined in a state of the ecosystem defined as the reference state (see below). The mean biomass flow $\Phi\tau$ and the mean speed of flow $K\tau$ for the reference state are deduced from the Ecopath parameters using the 2 following equations (Gascuel et al. 2008):

$$P\tau = \Phi\tau \times \Delta\tau \quad (S4)$$

$$K\tau = (P/B)\tau \quad (S5)$$

The inverse $1/K\tau$ parameter is equal to the life expectancy of organisms within their trophic class, and thus $K\tau$ depends on fishing and natural mortalities, the latter being related to the abundance of predators. Then, starting with values defined for the reference state, the $K\tau$ values are modified during simulations, according to the flow kinetic equation detailed in (Gascuel & Pauly 2009). The model also considers that only a fraction of the ecosystem biomass, called the accessible biomass B^*_τ (in t), is accessible to fisheries, due to ecological or technological reasons. Thus, starting with the reference state, EcoTroph allows users to simulate changes in the exploitation patterns, applying various effort multipliers to the accessible fishing mortality of reference F^*_τ (yr^{-1}), defined as the ratio between the catch and the accessible biomass.

LITERATURE CITED

- Badalamenti F, D'Anna G, Lopiano L, Scilipoti D and others (1995) Feeding habits of young-of-the-year greater amberjack *Seriola dumerili* (Risso, 1810) along the N/W Sicilian Coast. *Sci Mar* 59:317–323
- Barreiros JP, Santos RS, De Borda AE (2002) Food habits, schooling and predatory behaviour of the yellowmouth barracuda, *Sphyraena viridensis* (Perciformes: Sphyraenidae) in the Azores. *Cybium* 26:83–88
- Bell JD, Harmelin-Vivien L (1983) Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. 2. Feeding habits. *Tethys* 11:1–14

- Belsher T, Houlgatte E, Boudouresque CF (2005) Cartographie de la prairie à *Posidonia oceanica* et des principaux faciès sédimentaires marins du Parc national de Port-Cros (Var, France, Méditerranée). *Trav Sci Parc Nat Port-Cros* 21:19–28
- Berthon JF (1987) Relations trophiques entre quelques espèces d'échinodermes et le phytobenthos dans la baie de Port-Cros (Var, France). DEA in Océanologie Biologie, Université Pierre et Marie Curie, Paris
- Blanco S, Romo S, Villena MJ, Martinez S (2003) Fish communities and food web interactions in some shallow Mediterranean lakes. *Hydrobiologia* 506-509:473–480
- Cadiou G, Bonhomme P (2006) Suivi de l'effort de pêche professionnelle dans les eaux du Parc national de Port-Cros. Année 2005. Rapport No. 05-006.83400 PC, GIS Posidonie, Marseille
- Chakroun-Markouz N, Kartas F (1987) Denture et régime alimentaire des espèces du genre *Pagrus* (Pisces: Sparidae) des côtes tunisiennes. *Cybiurn* 11:3–19
- Chassot E, Mélin F, Le Pape O, Gascuel D (2007) Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. *Mar Ecol Prog Ser* 343:45–55
- Christensen V, Pauly D (1993) Trophic models of aquatic ecosystems. ICLARM, Manila
- Coll M, Palomera I, Tudela S, Sarda F (2006) Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, northwestern Mediterranean. *J Mar Syst* 59:63–96
- Costa MJ (1988) Ecologie alimentaire des poissons de l'estuaire du Tage. *Cybiurn* 12:301-320
- Donner M, Harrer D (2004) Ernährung und Nahrungsspezifität mediterraner Lippfisch-Arten (Labridae) und der Meeräsche *Oedalechilus labeo*. University of Innsbruck, Innsbruck
- Francour P (1990) Dynamique de l'écosystème à *Posidonia oceanica* dans le Parc National de Port-Cros. Analyse des compartiments matie, litière, faune vagile, échinodermes et poissons. Doctorat, Université Pierre et Marie Curie, Paris
- Francour P (1997) Fish assemblages of *Posidonia oceanica* beds at Port-Cros (France, NW Mediterranean): assessment of composition and long-term fluctuations by visual census. *PSZNI: Mar Ecol* 18:157–173
- Francour P (2007) Evolution pluriannuelle de la faune ichtyologique des substrats rocheux et de l'herbier à *Posidonia oceanica* du Parc National de Port-Cros (Var, Méditerranée nord-occidentale): analyse de la période 1988–2006. Rapport No. PNPC 04022 83400, LEMML, Université de Nice, Nice
- Frantzis A, Berthon JF, Maggiore F (1988) Relations trophiques entre les oursins *Arbacia lixula* et *Paracentrotus lividus* (Echinoidea Regularia) et le phytobenthos infralittoral superficiel dans la baie de Port-Cros (Var, France). *Trav Sci Parc Nat Port-Cros* 14:81–140
- Froese R, Pauly D (2009) FishBase. A global information system on fishes. Available at: <www.fishbase.org> (Version 11/2010)
- Gascuel D, Morissette L, Palomares MLD, Christensen V (2008) Trophic flow kinetics in marine ecosystems: toward a theoretical approach to ecosystem functioning. *Ecol Modell* 217:33–47
- Gascuel D, Pauly D (2009) EcoTroph: Modelling marine ecosystem functioning and impact of fishing. *Ecological Modelling (ECEM07, ECOMOD 5623)* 220:2885-2898
- Gramitto ME (1999) Feeding habits and estimation of daily ration of poor cod *Trisopterus minutus capelanus* (Gadidae) in the Adriatic Sea. *Cybiurn* 23:115–130
- Harmelin JG (1987) Structure et variabilité de l'ichtyofaune d'une zone rocheuse protégée en Méditerranée (Parc national de Port-Cros, France). *PSZNI: Mar Ecol* 8:263–284
- Harmelin JG, Garrabou J (2005) Suivi d'une population de *Paramuricea clavata* (Risso, 1826) (Cnidaria, Octocorallia, Gorgonacea) dans le Parc national de Port-Cros (Méditerranée, France): comparaison des états de 1992 et 2004 sur le site de la Galère. *Tra Sci Parc Nat Port-Cros* 21:175–191
- Harmelin JG, Harmelin-Vivien L (1999) A review on habitat, diet and growth of the dusky grouper *Epinephelus marginatus* (Lowe, 1834). *Mar Life* 9:11–20
- Harmelin JG, Ruitton S (2007) La population de corb (*Sciaena umbra*: Pisces) du Parc national de Port-Cros (France), état en 2005 et évolution depuis 1990: un indicateur halieutique et biogéographique pertinent. *Tra Sci Parc Nat Port-Cros* 22:49–65
- Hereu F (2004) The role of trophic interactions between fishes, sea urchins and algae in the northwestern Mediterranean rocky infralittoral. PhD thesis, Universitat de Barcelona, Barcelona
- Hoening J (1993) Empirical use of longevity data to estimate mortality rates. *Fish Bull* 81:898–903

- Kallianotis A, Torre M, Argyri A (2005) Age, growth, mortality, reproduction, and feeding habits of the striped seabream, *Lithognathus mormyrus* (Pisces: Sparidae), in the coastal waters of the Thracian Sea, Greece. *Sci Mar* 69:391–404
- Khoury C (1987) Ichtyofaune des herbiers de posidonies dans le Parc national de Port-Cros: composition, éthologie alimentaire et rôle dans le réseau trophique. Doctorat, Université de la Méditerranée, Marseille
- Linde M, Grau AM, Riera F, Massuti-Pascual E (2004) Analysis of trophic ontogeny in *Epinephelus marginatus* (Serranidae). *Cybium* 28:27–35
- Mackinson S (1999) System definition and primary production in mass-balance models of north-eastern Pacific ecosystems. In: Pauly D, Christensen V (eds) Fisheries Centre research reports, Vol 4, No. 1. Fisheries Centre, University of British Columbia, Vancouver, BC
- Macpherson E (1981) Resource partitioning in a Mediterranean demersal fish community. *Mar Ecol Prog Ser* 4:183–193
- Morales-Nin B, Moranta J (1997) Life history and fishery of the common dentex (*Dentex dentex*) in Mallorca (Balearic Islands, western Mediterranean). *Fish Res* 30:67–76
- Morato T, Sola E, Gros MP, Menezes G (2003) Diets of thornback ray (*Raja clavata*) and tope shark (*Galeorhinus galeus*) in the bottom longline fishery of the Azores, northeastern Atlantic. *Fish Bull* 101:590–602
- Morte MS, Redon MJ, Sanz-Brau A (2001) Feeding habits of *Trisopterus minutus capelanus* (Gadidae) off the eastern coast of Spain (western Mediterranean). *PSZNI: Mar Ecol* 22:215–229
- Ody D (1987) Les peuplements ichtyologiques des récifs artificiels de Provence (France, Méditerranée nord-occidentale). Doctorat, Université de la Méditerranée, Marseille
- Opitz S (1996) Trophic interactions in Caribbean coral reefs. Technical Report 43, ICLARM, Manila
- Palomares MLD, Pauly D (1998) Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Mar Fish Res* 49:447–453
- Pauly D (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J Mar Sci* 39:175–192
- Pinnegar JK (2000) Planktivorous fishes: links between the Mediterranean littoral and pelagic. Chapter 7: the ecological roles of planktivorous fishes in a Mediterranean rocky littoral system, evaluated using steady state modelling. PhD thesis in Marine Sciences and Coastal Management, University of Newcastle, Newcastle
- Rosecchi E (1983) Régime alimentaire du pageot, *Pagellus erythrinus*, Linne, 1758, (Pisces: Sparidae) dans le Golfe du Lion. *Cybium* 7:17–29
- Ruitton S, Le Diréach L, Charbonnel E (2004) Evaluation du peuplement de poissons de l'épave «La Barge aux Congres» du Parc national de Port-Cros. *Trav Sci Parc Nat Port-Cros* 20:211–230
- Russell RW, Harrison NM, Hunt JL (1999) Foraging at a front: hydrography, zooplankton, and avian planktivory in the northern Bering Sea. *Mar Ecol Prog Ser* 182:77–83
- Sala E, Ballesteros E (1997) Partitioning of space and food resources by three fish of the genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. *Mar Ecol Prog Ser* 152:273–283
- Santic M, Jardas I, Pallaoro A (2003) Feeding habits of Mediterranean horse mackerel, *Trachurus mediterraneus* (Carangidae), in the Central Adriatic Sea. *Cybium* 27:247–253
- Stergiou KI, Karpouzi V (2002) Feeding habits and trophic levels of Mediterranean fish. *Rev Fish Biol Fish* 11:217–254
- Vadon C (1981) Les Brachyours des herbiers de Posidonie dans la région de Villefranche. Doctorat, Université Pierre et Marie Curie, Paris
- Verlaque M (1990) Relations entre *Sarpa salpa* (Linnaeus, 1758) (Téléostéen, Sparidae), les autres poissons brouteurs et le phytobenthos algal méditerranéen. *Oceanol Acta* 13:373–388