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Top-down cascading effects driven by the odontocetes in the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea)

Ricci P.[1,2], Ingrosso M.[1], Cipriano G. [1,2], Fanizza C.[3], Maglietta R.[4], Renò V. [4], Tursi A. [1,2], Carlucci R. [1,2]

[1] Department of Biology, University of Bari, Via Orabona 4, Bari, Italy, email: pasquale.ricci@uniba.it; m.ingrosso14@studenti.uniba.it; giulia.cipriano@uniba.it; angelo.tursi@uniba.it; roberto.carlucci@uniba.it
[2] CoNISMa, Piazzale Flaminio 9, Rome, Italy
[3] Jonian Dolphin Conservation, Viale Virgilio,102 - 74121 Taranto, Italy, e-mail: carmelo@joniandolphin.it
[4] Institute of Intelligent Industrial Systems and Technologies for Advanced Manufacturing, National Research Council, Via Amendola 122 D/O, Bari, Italy, e-mail: rosalia.maglietta@cnr.it; vito.reno@cnr.it

***Abstract* – An investigation of the marine food web in the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea) was carried out to explore the top-down cascading effects driven by the Odontocetes. The food web was analysed by a mass-balance model using 51 functional groups and detailing the trophic impacts of the striped and common bottlenose dolphins, the Risso's dolphin and the sperm whale during the period 2010-2014. Odontocetes resulted top-predators with the highest TL estimated for the Risso's dolphin (TL=5.40) and the lowest for the common bottlenose dolphin (TL=4.47). The striped dolphin played the highest top-down control, showing cascading effects up to the 3rd TL. The Risso's dolphin and the sperm whale played similar cascading effects, but weaker than the striped dolphin. Understanding pattern and strengthen of trophic controls played by the Odontocetes within the food web could contribute to identify the basal mechanisms involved in the ecosystem functioning.**

I. INTRODUCTION

Predation changes the abundances of prey species influencing their interactions and behaviours in the basal levels of the food web [1]. Thus, the identification of top-down controls and their propagation towards the base of the food web is a critical point to assess the trophic cascades. In marine ecosystems, evidences of cascading effects have been detected in the pelagic domain [2], [3], [4] and the variability in the strength of cascades has been investigated [5]. However, the investigation of cascading effects in large marine ecosystems remains a critical issue due to the difficulty to apply field experiments, the scarcity of standardized data and the complexity of the food web. Not least, the methodological challenge of assessing ecosystem scale processes is also represented by the need to involve the field of marine ecology, fisheries and oceanography sciences with experts of analytic tools integrating several information [6]. In this contest, the ecological models based on holistic approach resulted more effective to describe the predation and fishing interactions in the trophic cascade process [7]. In particular, the mass-balance models allow to estimate indicators of both direct and indirect trophic impacts between the species (or group of species), providing information on the kind of trophic controls and their propagation through trophic levels.

Odontocetes, as top predators, are firmly recognized for their ecological role in the marine food webs [8]. This condition is generally ensured by their activation of trophic cascades, which are indirect strong top-down cascading effects played by the apex predators on two or more trophic levels [4]. However, the mechanism of such kind of activation and its strength, as well as the impact of fishing competition, the anthropogenic threats and the global change effects on the trophic cascades are still unknown in many marine ecosystems.

In the Gulf of Taranto (Northern Ionian Sea, Central Mediterranean Sea), a significant number of cetacean species coexist with several anthropogenic pressures, such as fishery, industrial discharges, marine traffic and navy exercise areas [9]. In particular, the striped dolphin (*Stenella coeruleoalba*, considered as "Vulnerable" in the IUCN Red List) results the most abundant species [10], followed by the common bottlenose dolphin (*Tursiops truncatus*), the sperm whale (*Physeter macrocephalus*) both listed as "Vulnerable" in the IUCN Red List and the Risso's dolphin (*Grampus griseus*, considered as "Data

Deficient" in the IUCN Red List) [11], [12]. These odontocetes were identified as apex predators and a keystone group in the food web of the North-western Ionian Sea [13], but information on the top-down controls played by each single species are still unknown. The main goal of this study is to explore the cascading effects driven by odontocetes and their top-down controls in the food web of the Gulf of Taranto.

II. MATERIALS AND METHODS

A. Study area

The Gulf of Taranto (GoT) is extended approximately for 14.000 km² in the Northern Ionian Sea (Fig. 1). The area is characterized by a complex geomorphology resulting in a large submarine canyon and sensitive habitats distributed in the shelf and deep zones. Several anthropogenic pressures insist on the basin such as fishery, navy exercises, marine traffic and industrial activities [9]. The food web model of the GoT included an area of about 7745 km^2 from Punta Alice up to S. Maria di Leuca, in a range of 10-800 m of depth.

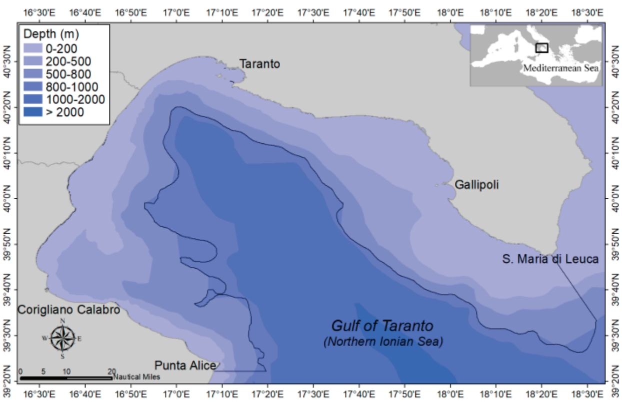

Fig. 1. The Gulf of Taranto in the Northern Ionian Sea. The modelled area (balck line) covers 7745 km^2

B. Food-web model approach and data collection

The Ecopath with Ecosim (EwE) modelling approach [14] was used to describe the mass-balance of the food web in the GoT. Food webs are described by means of Functional Groups (FGs), each representing a group of species with similar ecological traits, a single species or a life stage of a species. The FGs can represent consumers, autotrophs and non-living compartments (e.g. organic matter), and links between FGs are formally described by a set of linear equations, one for each FG, representing the balance of energy and matter expressed as:

$$B_i \cdot \left(\frac{P}{B}\right)_i * EE_i - \sum_{j=1}^{n} B_j * \left(\frac{Q}{B}\right)_j * DC_{ij} - Y_i - E_i - BA_i = 0 \quad (1)$$

where B_i is the biomass of group (i), $(P/B)_i$ is the production of (i) per unit of biomass; the consumption i by the other FGs of the food web is then represented through $(Q/B)_j$ the consumption per unit of biomass of all j predators the proportion of (i) in the diet composition of predator (j) in terms of biomass (DC_{ij}); other losses on group i are represented by fishery catches Y_i; the net migration rate E_i and eventually the biomass accumulation BA_i. The parameter EE_i represents the ecotrophic efficiency, i.e., the proportion of the production of group (i) which is utilized within the system modelled [15]. Energy balance for each group is also ensured by equating its consumption (Q/B_i) with the sum of production (P/B_i), respiration (R/B_i) and unassimilated food ($U/Q*Q/B_i$). The system of equations is solved according to several ecological constrains by providing EwE with diet composition, the unassimilated food, the catches, the exports for each group and three of the basic parameters B_i, $(P/B)_i$, $(Q/B)_i$ and EE_i [14]. The solution provides a snapshot of the trophic flows within the ecosystem (further details on EwE modelling approach can be found in review literature as [15], [16].

A total 51 FGs described the GoT food web detailing the pelagic, demersal, benthic, planktonic domains (or compartments). The striped and common bottlenose dolphins, Risso's dolphin and sperm whale were represented as 4 individual FGs. The demersal and benthopelagic domains are described by a total of 276 species sampled during the "MEDiterranean International Trawl Survey" (MEDITS time series 1995-2015, [17]) successively been aggregated into 29 FGs identified by a reiterative aggregation method, based on similarity in quantitative diet information and the bathymetric distribution of species [13]. Moreover, a total of 5 FGs described the planktonic domain (the phytoplankton, the bacterioplankton, the macrozooplankton, the meso-microzooplankton and the gelatinous plankton); 6 FGs the pelagic domain (the fin whale [18], the loggerhead turtle, the seabirds and the large, medium and small pelagic fishes) and, 4 FGs the benthic domain (the macrobenthic invertebrates, the polychaetes, the suprabenthic crustaceans and the seagrasses and seaweeds). In the last, the non-living matter was represented by 3 groups.

The GoT model was developed for a period of 4 years (2010-2014) using a wide set of input data obtained from several data collections. The diets used for *S. coeruleoalba*, *T. truncatus* and *G. griseus* were mostly derived from the stomach contents analysed in the North Aegean Sea [19]. Starting from these diets used as a baseline, additional food items were also integrated from the literature, when available, to improve the robustness of the input information. In fact, for *T. truncatus* and *G. griseus* food items were added from the Western Mediterranean areas [20], [21], whilst for *S. coeruleoalba* from the Ionian Sea [22]. The diet information for the *P. macrocephalus* was derived from the Ligurian Sea [23].

The biomass estimates of the 4 investigated odontocetes were derived from abundance data (N·km^{-2}) collected during monitoring surveys carried out in the Gulf of Taranto since 2009 [10], [24] and values of mean individual weight [13]. Biomass estimates (in t km^{-2} of wet weight) for many fish species, cephalopods and crustaceans were obtained from the MEDITS trawl surveys carried out during the period 1995-2015 [13]. The biomasses, diet information and productivity and consumption rates of all other FGs were obtained by the previous food web model realized in the area [13].

The fishing activities were described by 5 fishing gears: trawls, long lines, nets, other gears and purse seines. Landings for each gear by species were obtained by the Fisheries and Aquaculture Economic Research for the Ministry of Agricultural Food and Forestry Policies (MIPAAF). Discard was estimated by the available discard rates in literature [25], [26] and using the proportion of commercial and non-commercial discards in MEDITS catches for the no commercial species harvested by the trawl [13].

Balancing steps of the model were carried out to assess the coherence of the input data with the basic thermodynamic laws, rules and principles of ecosystem ecology at the system level [16].

C. Ecological Indicators

The trophic level (TL, [27]) is calculated by the following equation:

$$TLi = 1 + \sum_j (TL_j * DC_{ij}) \qquad (2)$$

TL is a fractional number giving the position of each functional group in its food web, and estimated by Ecopath based on the diet composition (DC) of the group and the TL of its prey items (starting with a TL of 1 assigned to producers and detritus).

The top-down controls and the importance of the odontocetes in the food web were assessed by means the Mixed Trophic Impact analysis (MTI, [28]) and the Keystoness Index (KS). The MTI quantifies the relative impact of biomass change within a component (impacting group) on each of the other components (impacted groups) in the food web. Positive/negative MTI values indicate an increase/decrease in biomass of the group j due to a slight increase in biomass of the impacting group i. Therefore, negative impacts can be associated to prevailing top-down effects and positive ones to bottom-up effects [29]. The MTI provides estimates of the overall effect (ε_i) of the trophic impact component, that together with the relative biomass component (p_i) is used to estimate KS. The overall effect of a group i represents all the direct or indirect trophic impacts of group i on all the other groups in the food web:

$$\varepsilon_i = \sqrt{\sum_{j=1}^{n} m_{ij}^2} \quad (3)$$

where the impact on the group itself (m_{ij} with i=j) is not considered, and ε_i is calculated as a relative value with respect to the maximum [29]. The parameter p_i is the relative biomass of the group in the food web, excluding detritus biomass:

$$p_i = \frac{B_i}{\sum_{k=1}^{n} B_i} \qquad (4)$$

Thus, the KS is expressed as:

$$KS_i = IC_L \times BC_0 \qquad (5)$$

where IC_L (Impact Component) is estimated by means of the ε_i and BC_0 (the Biomass Component) is estimated from p_i, where BC_0 is the biomass in a descending order ranking [30]. In order to assess the cascading effects along the TLs due to the top-down controls of the Odontocetes, the MTI values of each FGs impacted by the Odontocetes (m_{ij} with i=cetaceans and j=all other FGs) was weighted with the proportion of flows of group j belonging to integer TLs calculated by Ecopath' s routine. In addition, the trophic impacts were assessed at scale of domains: Pelagic, Demersal (Shelf, Shelf- Break and Slope), Benthic and Planktonic. FGs impacted by the odontocetes were aggregated in their own domains. In the end, direct positive impacts on the preys were assessed for each odontocetes, in order to identify the condition of "beneficial predator" [28]. Direct impacts were considered as the impacts on the FGs consumed by the odontocetes (identified by the preys in their diet information).

III. RESULTS

Odontocetes resulted top-predators within the GoT food web, with the highest TLs estimated for the Risso's dolphin (TL=5.40) and the sperm whale (TL=5.16), followed by the striped dolphin (TL=4.71) and common bottlenose dolphin (TL=4.47).

The striped dolphin showed the highest value among odontocetes (KS=1.31) resulting in the 2nd position of the KS rank. The Risso's dolphin was in the 4th position (KS=1.13), the sperm whale in the 11th (KS=0.89) and the common bottlenose dolphin in the 15th (KS=0.84). The 1st position in the rank was occupied by the bathyal squids (e.g. *Todarodes sagittatus*, *Histioteuthis* spp.).

The striped dolphin played the highest negative and positive impacts, which showed a clear cascading effect up to the 3rd TL (Fig. 2). The Risso's dolphin and sperm whale showed similar cascading effects, but with values smaller than the striped dolphin. All these species exerted negative impacts higher than their positive ones on the FGs placed in the 5th and 4th TLs. On the contrary, the positive impacts on the groups of the 3rd TL resulted higher than the negatives. The common bottlenose dolphin showed negative impacts on the groups of the 3rd TL but without a clear pattern in the cascading effects.

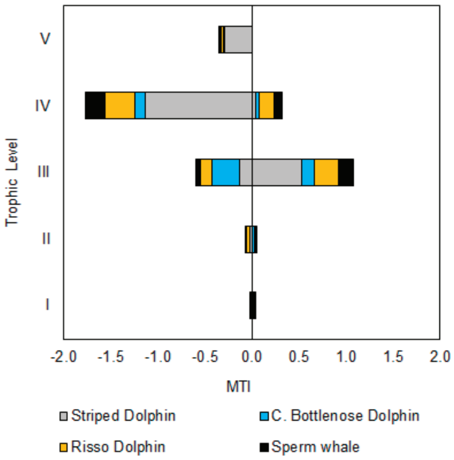

Fig.2. The Mixed Trophic Impact (MTI negative and positive) estimated for the odontocetes with the FGs impacted aggregated by discrete trophic levels.

The striped dolphin showed both the highest negative and positive impacts on the pelagic FGs (< −0.5) and on all demersal FGs (> 0.1), respectively (Fig. 3). High negative impacts were also detected on the shelf-break and slope demersal FGs. *T. truncatus* played negative impacts on all demersal FGs and small positive impacts on all domains, excluding the benthic one. *G. griseus* showed its highest negative and positive impacts on the slope demersal FGs, and positive impacts were detected on both pelagic and the shelf and shelf-break demersal FGs. *P. macrocephalus* played high negative impacts on both the pelagic and slope demersal FGs. Excluding the *T. truncatus*, all odontocetes exerted small negative impacts on the planktonic FGs.

Striped dolphin was the most important beneficial predator, with direct positive impacts on 9 FGs, such as bathyal benthic cephalopods (e.g. Sepiolidae), shelf demersal benthivorous fishes (e.g. *Mullus surmuletus*, *Pagellus acarne*, *Gobius* spp.) and Macrourids.

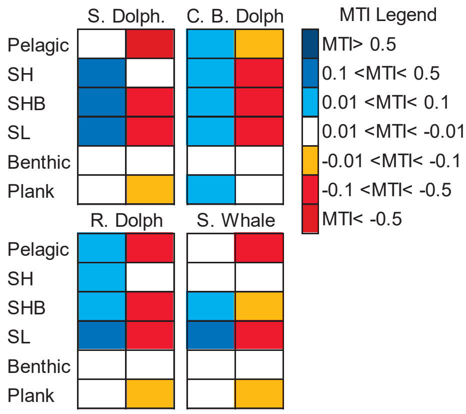

Fig.3. The Mixed Trophic Impact (MTI negative and positive) estimated for the odontocetes with the FGs impacted aggregated in Pelagic, Demersal (Shelf SH, Shelf- Break SHB and Slope SL) Benthic and Planktonic (Plank) domains.

IV. DISCUSSIONS AND CONCLUSIONS

This study represents an attempt to identify top-down controls played by the Odontocetes detailing the pattern and strength of cascading effects induced by their predation activities in the food web of the Gulf of Taranto. The trophic levels estimated for the Odontocetes (TL>4.4) indicated their status of apex predators generally in line with the trophic levels estimated in the Mediterranean areas [31]. The role of striped dolphin in the top-down cascading effects resulted more evident than those estimated for other Odontocetes. Likely, this condition is due to its greater abundance in the study area, where the species performs its entire life cycle [10], [24]. In addition, the feeding preferences and the magnitude of trophic interactions of *S. coeruleoalba* could be another key element. In fact, the striped dolphin plays top-down controls on other keystone species distributed in the middle trophic levels (e.g. mesopelagic fishes and small bathyal squids). Preferential trophic interactions could also explain the cascading effects detected for the Risso's dolphin and sperm whale. In fact, both species are characterized by a specific predation on the bathyal squids, which are the most important keystone species identified in the food web. This strong interaction between large Odontocetes and benthopelagic cephalopods was observed in western Mediterranean Sea by means similar food web models [32]. Moreover, the top-down cascading effect induced by the predation of the sperm whale on the large squids was detected in the Pacific Ocean [33]. Notably, the cascading effects have been detected up to the third trophic level, while below this level the effects seem to be very negligible. This observation was also detected in the analysis on the planktivorous fishes, zooplankton and phytoplankton interactions [3]. Not least, the dominance of bottom-up controls (resource limitation) in the marine systems could be a masking factor of the top-down controls [6]. However, in peculiar contexts, where a great decrease of dolphins and overfishing conditions are simultaneous, the strength of this control can be amplified and the cascading effects can also influence the phytoplankton abundance, as reported in the Black Sea [7]. Although the strength of top-down controls seems to vanish below the 3rd levels, weak negative effects have been detected on the planktonic domain. This observation has been provided by the assessment of the top-down controls aggregating the impacted FGs in the domains. Thus, effects due to the predation activities seems also to propagate in different compartments and along the depth gradient. For instance, even if the striped dolphin feeds on mesopelagic preys distributed on the slope, they determined positive effects even on the shallowest demersal species. However, further investigations are required to better understand the mechanisms of this propagation, which are linked to the degree of connectance among species, the feeding strategies and the changes in the preys' and predators' distribution during the life-cycles [34].

Finally, the condition of beneficial predator identified for the striped dolphin represents a new observation for the food web in the investigated area, highlighting the importance of the predation on the equilibrium dynamic of the trophic structure.

The understanding of the relationships between trophic controls played by the odontocetes and the changes in the species abundance in the food web could contribute to identify the basal mechanisms involved in the ecosystem functioning. The knowledge obtained by such kind of studies seems to be very informative mostly for the implementation of conservation and management plans of marine resources according to the goals for Sustainable Development of the United Nations (Goal 14, Life below water) [35] and the EU Marine Strategy Framework Directive [36].

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