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Research Note

Towards a framework for assessment and management of cumulative human impacts on marine food webs

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Abstract: *Effective ecosystem-based management requires understanding ecosystem responses to multiple human threats, rather than focusing on single threats. To understand ecosystem responses to anthropogenic threats holistically, it is necessary to know how threats affect different components within ecosystems and ultimately alter ecosystem functioning. We used a case study of a Mediterranean seagrass* (Posidonia oceanica) *food web and expert knowledge elicitation in an application of the initial steps of a framework for assessment of cumulative human impacts on food webs. We produced a conceptual seagrass food web model, determined the main trophic relationships, identified the main threats to the food web components, and assessed the components' vulnerability to those threats. Some threats had high (e.g., coastal infrastructure) or low impacts (e.g., agricultural runoff) on all food web components, whereas others (e.g., introduced carnivores) had very different impacts on each component. Partitioning the ecosystem into its components enabled us to identify threats previously overlooked and to reevaluate the importance of threats commonly perceived as major. By incorporating this understanding of system vulnerability with data on changes in the state of each threat (e.g.,*

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decreasing domestic pollution and increasing fishing) into a food web model, managers may be better able to estimate and predict cumulative human impacts on ecosystems and to prioritize conservation actions.

Keywords: conservation actions, ecosystem-based management, expert knowledge elicitation, multiple threats, seagrass, vulnerability

Hacia un Marco de Trabajo para la Evaluación y el Manejo de los Impactos Humanos Acumulativos sobre las Redes Alimenticias Marinas

Resumen: *El manejo efectivo con base en los ecosistemas requiere entender la respuesta de los ecosistemas a múltiples amenazas humanas en lugar de enfocarse en amenazas individuales. Para entender holísticamente la respuesta de los ecosistemas a las múltiples amenazas antropogénicas es necesario saber cómo estas amenazas afectan a los diferentes componentes dentro de los ecosistemas y cómo alteran finalmente el funcionamiento de los ecosistemas. Usamos el estudio de caso de la red alimenticia del pasto marino del Mediterráneo* (Posidonia oceanica) *y la obtención de conocimiento de expertos en una aplicación de los pasos iniciales de un método para la evaluación de los impactos humanos acumulativos sobre las redes alimenticias. Produjimos un modelo de red alimenticia de pastos marinos, determinamos las principales relaciones tróficas, identificamos a las principales amenazas para los componentes de la red y evaluamos la vulnerabilidad de los componentes a esas amenazas. Algunas amenazas tuvieron impactos altos (p. ej.: infraestructura costera) o bajos (p. ej.: escorrentía agrícola) sobre todos los componentes de la red, mientras que otros (p. ej.: carnívoros introducidos) tuvieron impactos muy diferentes sobre cada componente. Partir al ecosistema en sus componentes nos permitió identificar amenazas no vistas previamente y reevaluar la importancia de las amenazas percibidas comúnmente como mayores. Al incorporar este entendimiento de la vulnerabilidad del sistema con datos sobre los cambios en el estado de cada amenaza (p. ej.: disminución de la contaminación doméstica e incremento de la pesca) al modelo de red alimenticia, los manejadores pueden ser capaces de estimar y predecir de mejor manera los impactos humanos acumulativos sobre los ecosistemas y priorizar las acciones de conservación.*

Palabras Clave: acciones de conservación, amenazas múltiples, manejo con base en los ecosistemas, obtención de conocimiento de expertos, pastos marinos, vulnerabilidad

Introduction

Ecosystems are affected by multiple human threats simultaneously (Halpern et al. 2008*a*). Recently, there has been increased emphasis on ecosystem-based management (EBM) approaches to address this challenge. EBM aims to sustain ecosystems and their services to humans considering the complexity of human pressures on ecosystems (Levin et al. 2009).

Management decisions ideally should be guided by an understanding of how ecological components or specific ecosystem services respond to multiple threats in a given location. Management actions that focus on threat mitigation will have different and, sometimes, contradictory consequences for different ecosystem components and services based on how directly or indirectly those ecosystem attributes are affected by the threat (Halpern et al. 2008*b*), and on how each service is linked to specific ecosystem components. Thus, for effective and efficient EBM implementation, it is important to understand not only how anthropogenic threats diffuse across space, but also how those threats affect different components within complex ecosystems, ultimately affecting ecosystem structure and functioning. To date, cumulative impact assessments have focused on entire ecosystems, essentially averaging the effect across all species (e.g., Halpern et al. 2008*a*; Ban et al. 2010) or on single species or taxa (e.g., Maxwell et al. 2013). We devised a framework that accounts for food web interactions (Fig. 1) to better understand how human threats affect different ecosystem components and consequently ecosystem functioning. We used a food web of the endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile ecosystem as a case study in which we applied steps 1–4 of our proposed method (Fig. 1). To assess the vulnerability of food web components to multiple threats, we applied an expert knowledge elicitation method. In the absence of sufficient empirical data, expert knowledge elicitation has emerged as a key tool for rational decision making in conservation (Burgman et al. 2011). Our framework should be relevant and applicable to other ecosystems at any location.

Methods

Case Study

In the Mediterranean Sea, meadows formed by *P. oceanica* are widespread, spanning the coastal waters of 16 countries, but they have been subjected to rapid decline over the past decades (Giakoumi et al. 2013). The *P. oceanica* ecosystem has been studied more than any other in the Mediterranean; there are more than 2100 ISI publications (search on Web of Science for the period

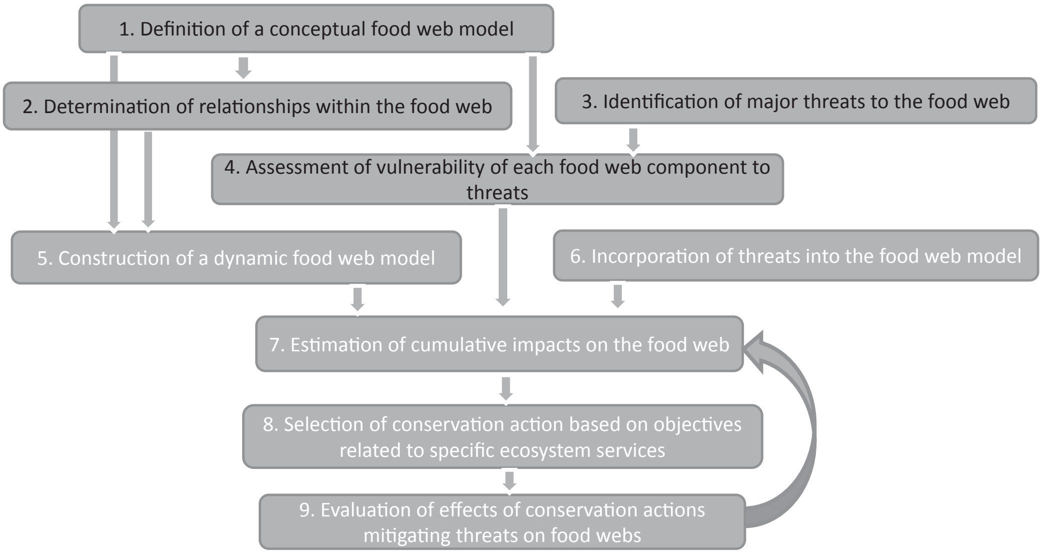

Figure 1. Framework for the selection of management actions accounting for cumulative human impacts on food webs. Steps 1 to 4 (black type) are presented through the seagrass case study, and steps 5–9 are discussed.

1864–2014) and a substantial amount of gray literature on the ecosystem (e.g., Boudouresque et al. 2012). Yet, empirical data are still missing regarding the vulnerability of various components of the seagrass food web to human threats. Therefore, an expert knowledge elicitation process was followed to obtain information.

Expert Knowledge Elicitation

We convened a 3-day workshop of 14 experts on the *P. oceanica* ecosystem and its threats in 2013 to acquire information that would allow us develop the initial steps of a framework for assessing cumulative human impacts on food webs. Before and during the workshop, expert knowledge was used to identify: the main components of the seagrass food web; the relationships among these components; the main human threats to the food web; and the vulnerability of the different components of *P. oceanica* food web to human threats (see Supporting Information for elicitation process description and summary of literature review). Experts consulted the conceptual *P. oceanica* food web in Personnic et al. (2014) and key references that describe trophic relationships in the *P. oceanica* ecosystem (e.g., Buia et al. 2000; Vizzini 2009).

Vulnerability Assessment

To assess each components' vulnerability to human threats, we used vulnerability measures based on those developed by Halpern et al. (2007) for ecosystems and Maxwell et al. (2013) for marine predators. The 4 adapted vulnerability measures were scale of impact, frequency of impact, sensitivity to the impact, and recovery time (Supporting Information). Scale and frequency of impact define level of exposure to the impact of a threat, sensitivity is the likelihood and magnitude of an impact on a food web component once the impact occurs, and recovery is the adaptive capacity of the food web component. We assessed level of certainty (i.e., available evidence) for each food web component and threat interaction. We took the grand mean of these weighted averages of the 4 vulnerability measures to get a single score (from 0 to 4) that indicated how a given threat affects a particular food web component (Supporting Information).

Framework Steps 1–4

The information acquired by the experts and the development of the vulnerability assessment method described allowed us to implement the first 4 steps of the proposed framework (Fig. 1). We produced a static food web model that encompassed the major trophic groups in the seagrass ecosystem (step 1). We considered tradeoffs between complexity and data availability. Then, we defined the major trophic interactions and organic matter flows in the system (step 2). We also identified the major threats to each ecosystem component (step 3). To address the challenge of tracking impacts on different food web components, we teased apart the direct and indirect responses of ecosystem components to each threat type (step 4). This step is necessary to produce a more comprehensive understanding of why and how ecosystems respond to the cumulative impact of human activities at a later stage (step 7 in Fig. 1).

Results

Conceptual *P. oceanica* Food Web Model and Trophic Relations

Experts identified the principal components of the *P. oceanica* food web (step 1) and major trophic

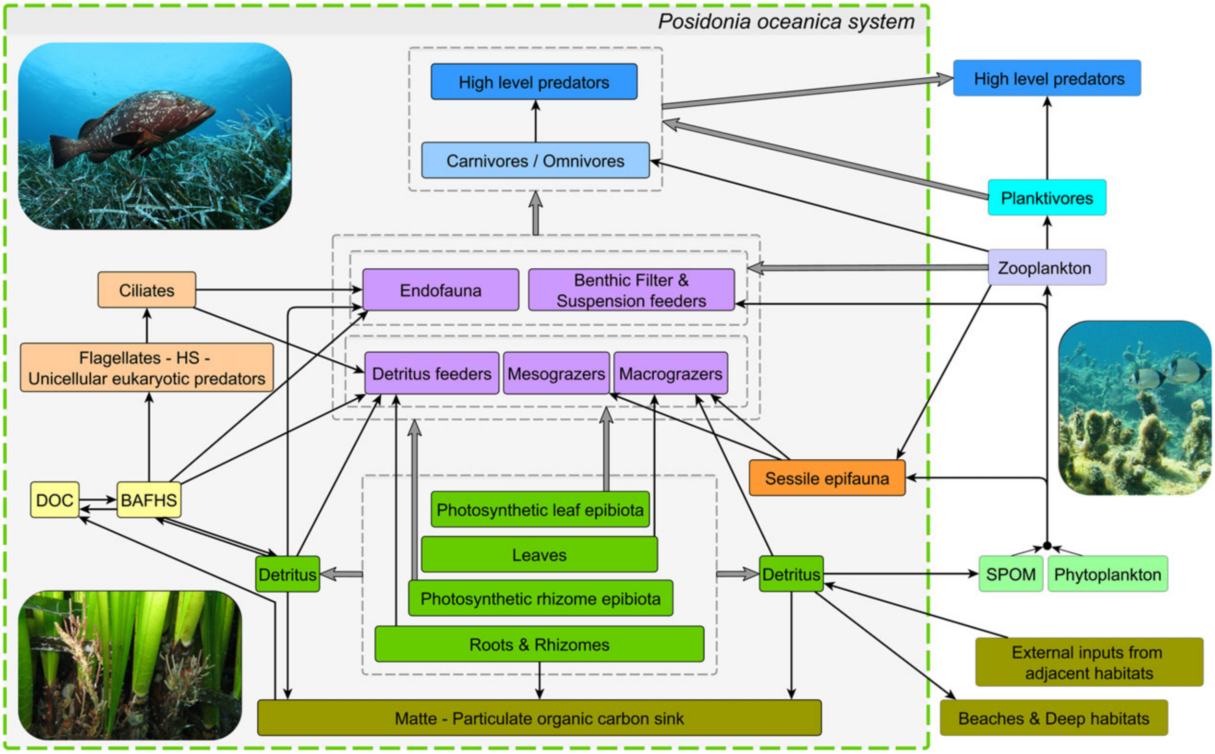

Figure 2. Conceptual P. oceanica *food web model (colored rectangles, food web components; outer green dashed line,* P. oceanica *system; gray dashed line, clusters of functional groups that share a common link to some other compartments; black arrows, transfer of energy among different compartments; gray arrows, energy transfer among clusters of food web components; DOC, dissolved organic carbon; BAFHS, bacteria, archaea, fungi, and heterotrophic stramenopiles; SPOM, suspended particulate organic matter). Top left picture courtesy of S. Ruitton.*

interactions and organic matter flows in the system (step 2). The model included functional compartments from producers to high-level predators (Fig. 2 & Supporting Information).

Main Threats and Food Web Components' Vulnerability

Experts identified 21 main human threats on the *P. oceanica* ecosystem (step 3), 9 of which are sea-based and 12 of which are land-based (see Supporting Information for threats' definitions). Some threats appeared to have high impacts on all food web components (Fig. 3, right-hand side), whereas others had lower and very different impacts across functional compartments (e.g., introduced herbivores, climate change—sea-level rise). A third group had even lower effects on all components (e.g., introduced carnivores, agricultural runoff) (step 4). All threats related to climate change, except for acidification, presented a high variation in their impacts across functional compartments, possibly reflecting limited available information.

The majority of food web components were most vulnerable to broad-scale irreversible coastal construction, such as ports, except for carnivores and omnivores and high-level predators. Carnivores and omnivores and high-level predators seemed to be more vulnerable to trawling and other fishing techniques, respectively, because these components are specifically targeted by such activities. Large fish farms, through increased sedimentation, nutrient load, and light restriction, were believed to be a second major threat for *P. oceanica* leaf canopy and associated epibiota, but to have less influence on higher trophic levels (Fig. 3). For most organisms, except for endofauna, trawling was among the top 5 threats. However, its rank differed among functional compartments. Industrial pollution was also among the top 5 threats for all food web components. Figure 3 shows also the threats food web components were less vulnerable to. However, such low vulnerability should be treated with caution because most of the low-ranked threats (e.g., agricultural runoff and sea-level rise) had the least certainty (Supporting Information).

Gaps in Knowledge

According to experts, *P. oceanica* leaves were the best documented food web component in terms of impacts from human threats followed by epibiota, *P. oceanica* roots and rhizomes, and macrograzers. The most poorly documented components were: endofauna, filter

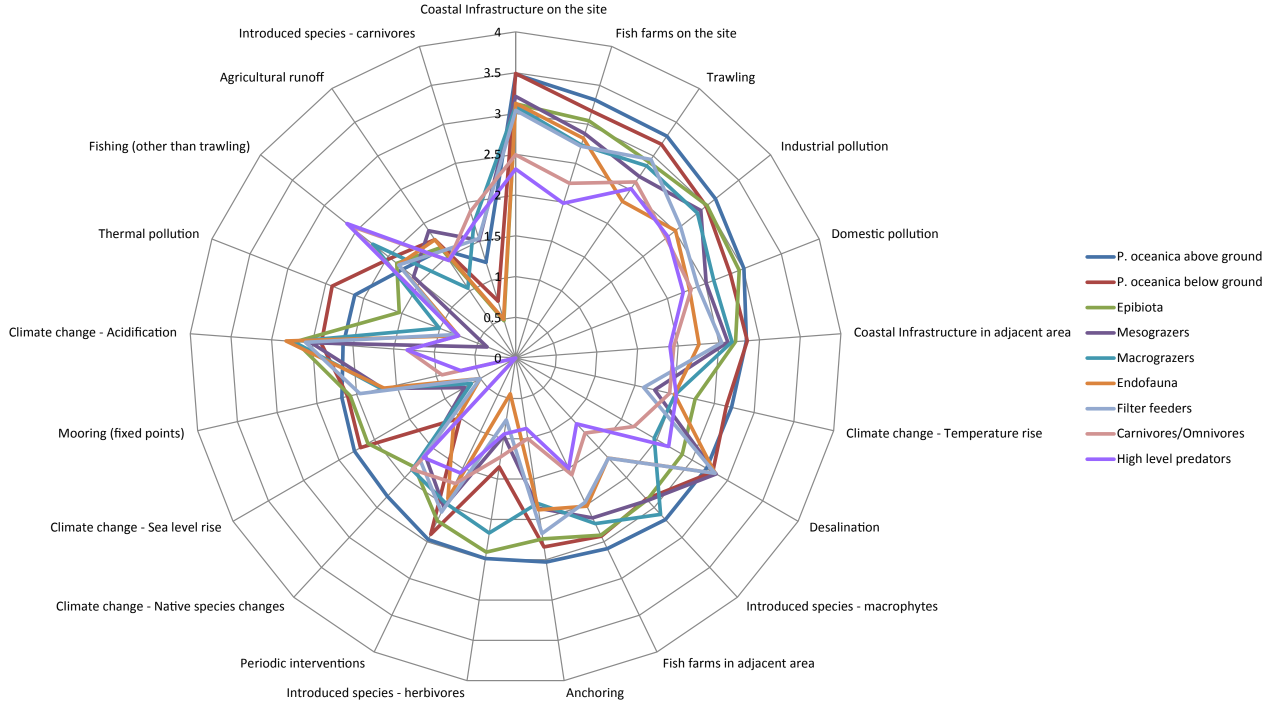

Figure 3. Radar chart of the relative vulnerability (0 [lowest] to 4 [highest]) of P. oceanica *food web components to human threats. Each food web component is a different color and each threat corresponds to a spoke.*

feeders, and high-level predators. Overall, the impacts with the greatest level of certainty were related to the following threats: fish farms, irreversible coastal infrastructure, domestic pollution, and trawling. In contrast, information on impacts was almost nonexistent for threats such as agricultural runoff, thermal pollution, introduced carnivorous species, and sea-level rise. Impacts from anchoring, fish farming (in adjacent area), and introduction of alien macrophytes could be more or less certain depending on whether they affected lower or higher trophic levels. Unsurprisingly, the greatest variation in the scores attributed by experts to vulnerability measures was observed for the most poorly studied food web components and threats (Fig. 2 & Supporting Information).

Discussion

Marine coastal ecosystems are threatened by multiple land- and sea-based threats acting in concert. Our results show that food web components differ in their vulnerability to human threats and are expected to react in different ways when exposed to them. These results can be the basis of more accurate predictions of how human impacts affect ecosystem components. When such information is incorporated into a trophic model that includes trophic dynamics, one can obtain a more precise estimate of how overall ecosystems will respond to the cumulative effect of anthropogenic threats. Consequently, detailed knowledge of the impacts of threats on ecosystems can identify threat mitigation actions with potential benefits to ecosystems and their ability to deliver desired ecosystem services. EBM should be more effective if it were to take into account direct and indirect impacts of threats to different ecosystem components, rather than using ecosystem-wide or taxa-specific measures of impacts (Carey et al. 2014).

Partitioning the ecosystem into its components facilitated the identification of main threats to the ecosystem as a whole. For instance, when threats to *P. oceanica* ecosystem were initially identified based on Boudouresque et al. (2009), fishing practices (other than trawling) were not included as a major threat on *P. oceanica* because the focus of that review was the plant itself and not the food web. However, when considering all ecosystem components, this threat was added because it directly threatens higher trophic levels of the food web. This has implications in prioritizing actions for the maintenance of ecosystem services. More specifically, the objective of maintaining seagrass meadows as a source for food provision may prioritize restrictions to fishing practices as an appropriate management action.

In contrast, threats widely considered as major threats to seagrasses, such as agricultural runoff (Grech et al. 2012), appeared to be less important for *P. oceanica* (Fig. 2), whose meadows are always absent from areas near large river discharges due to low salinity. In the absence of empirical data, experts attributed very low certainty to the impacts of this threat on all food web components. Such findings are particularly important from a management point of view because further research is needed to assess the impacts of agricultural runoff on *P. oceanica* before investing conservation resources to mitigate this threat. The lack of impact assessment impairs the estimation of potential benefits from conservation actions mitigating this threat. At the same time, actions directed to address other threats where the impacts are more certain may be more efficient and reduce the risk of failure.

Food web components showed a great variation in expected vulnerability to climate change–related threats. This variation reflects the low level of certainty regarding the impacts of climate change on most functional compartments and the need for further research in this field. Overall, ecosystem components seemed to be more vulnerable to local rather than global threats. This finding contrasts with evidence from previous studies in the region (e.g., Micheli et al. 2013) and elsewhere (e.g., Ban et al. 2010). Certainty about the impacts of threats on whole ecosystems seems to decrease when experts focus on impacts to each ecosystem component separately. Just as segregating vulnerability into its components can provide a more accurate estimate of an ecosystems' vulnerability to threats (Halpern et al. 2007), identifying human impacts on each ecosystem component can help in the estimation of overall impacts of threats on ecosystems and provide insights on how these can be mitigated.

To assess the overall benefits of different sets of management actions on food webs, additional steps are needed (Fig. 1). A further step is the construction of a quantitative food web model from data on the biomass of functional compartments and fluxes between compartments (step 5). Interactions among organisms or functional compartments within food webs that are precipitated by the introduction or removal of multiple threats (step 6) will determine the cumulative impacts on the food web (step 7). When a full model is available, relations between threats (synergistic, antagonistic, or additive) can be quantified taking into account the structure of the food web and its dynamics. Then, the vulnerability values of food web components to human threats estimated here can be incorporated into the dynamic food web model for the parameterization of each food web component. Efficient prioritization of resources demands that actions to address specific threats and their corresponding costs and conservation benefits be identified (Evans et al. 2011). Better estimation of cumulative impacts on the food web will allow better estimation of conservation benefits resulting from management actions (steps 8 and 9).

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Supporting Information

Methods of expert knowledge elicitation and vulnerability assessment, the expert questionnaire, a summary of the literature review, threats definition, and threat relations to stressors (Appendix S1), as well as a detailed description of the food web (Appendix S2) and an illustration of uncertainty for food web component and threat combinations (Appendix S3) are available on-line. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Appendix S1: Methods including a) Expert knowledge elicitation, b) Vulnerability assessment, c) experts' questionnaire, d) literature related to impacts of threats on functional compartments (Table S1.2), e) threats definitions, as well as ranks of vulnerability measures (Table S1.1) and threats – stressors table (S1.3)

a) Expert knowledge elicitation

Experts were selected by assessing the scientific literature on the impacts of threats on the *P. oceanica* ecosystem. Experts' experience of the *Posidonia oceanica* ecosystem ranged from 2 to 35 years, with an average of 19 years. A Nominal Group Technique (NGT) was followed (Van de Ven & Delbecq 1971, 1974) and consisted of three stages: 1) estimate, 2) feedback, and 3) re-estimate. Experts were asked to fill in a questionnaire prior to their attendance to the workshop, in order to elicit information from them independently. The questionnaire required evaluation of the vulnerability of food web components to a number of threats. The initial selection of food web components and threats was based on Boudouresque et al. (2009, 2012). Facilitated face-to-face group discussions followed during the workshop. Experts were shown a visual summary of responses from all participants and discussed about the initial evaluations, which later allowed them to update their values. Experts were not required to form a single group estimate, but to provide arguments for their initial evaluations.

During the workshop, the principal components of the seagrass food web and their main threats were discussed and revised (see definitions and threats/stressors relations in part E; pages 26-28). Furthermore, a part of the workshop was dedicated to an update of the conceptual representation of the *P. oceanica* food web and the identification of trophic relations between components. After workshop discussions, questionnaires were modified according to experts' suggestions, and experts were asked to make individually second final private estimates (see questionnaire on pages 6-17). Experts had access to literature containing empirical data for all food web components/threat combinations available (Table S1.2). This list of references was the product of an extensive search in ISI Web of Knowledge (period covered 1864 – 2014) using within the ‘‘Topic” field a combination of threats and food web components (i.e. names of family, genus or species belonging to each food web component) as keywords. We retrieved numerous studies on the impacts of threats on *P. oceanica* food web components across the Mediterranean Sea at various spatial scales (see Table S1.2, pages 18 &19).

b) Vulnerability assessment

Values for each component/threat combination were obtained using methods described in Halpern et al. (2007). For each vulnerability measure and each of the 189 component/threat combinations, we resized “scale” and “sensitivity” values to range from 0 to 4, so that all vulnerability measures are in the same scale (Table S1.1). Average scores across experts' responses for each component (*i*) / threat (*j*) combination were estimated by: 1) multiplying the 0-4 rank given by each expert (x_{ij}) by the corresponding certainty value (c_{ij}), and 2) dividing the sum of these weighted values for each vulnerability measure by the sum of the certainty values provided by the experts:

$$\bar{x} = \frac{\sum_{\substack{1\leq i \leq m \\ 1\leq j\leq n}} x_{ij}\, c_{ij}}{\sum_{\substack{1\leq i \leq m \\ 1\leq j\leq n}} c_{ij}}$$

Then, we took the grand mean of these weighted averages of the four vulnerability measures to get a single score (from 0 to 4) that indicated how a given threat affects a particular food web component (see Halpern et al. 2007 for a detailed description). We assumed equal weighting of the four vulnerability measures because it is difficult to attribute them different weights based on available information: each plays an important and variable role depending on the threat considered and context (Halpern et al. 2007). Vulnerability was assessed for the most important and well-studied components described in the conceptual model of the *P. oceanica* food web.

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Table S1.1: Ranks of vulnerability measures for impact assessment on food web components.

Vulnerability measure	Category	Rank	Descriptive Notes	Example
Scale (m^2) ***What is the scale of the threat impact?***	No threat	0		
	<10	1		Anchor damage
	10-100	2		Reduced light due to fish farm pens
	100-1000	3		Sediment runoff
	1000-10000	4		Single trawl drag
	>10000	5		Land-based pollution from runoff of rivers
Frequency ***What is the frequency of the impact?***	Never	0		
	Rare	1	Infrequent enough to affect long-term dynamics of a given population or location	Large oil spill
	Occasional	2	Frequent but irregular in nature	Toxic algal blooms
	Annual or regular	3	Frequent and often seasonal or periodic in nature	Runoff events due to seasonal rains
	Persistent or permanent	4	More or less constant year-round lasting through multiple years or decades	Coastal infrastructure
Sensitivity	No impact	0		

How likely is that impact to affect the species in the affected trophic level?	Low	1	Unlikely to result in change in cover, density, abundance or community structure (0-33%)	Anchor damage
	Medium	2	Moderate likelihood of change in cover, density, abundance or community structure (33-66%)	Introduction of invasive species
	High	3	High likelihood of change in cover, density, abundance or community structure (66-100%)	Use of explosives in fishing
Recovery time (years) ***How long does it take to recover from exposure to the impact?***	No impact	0		
	<1	1		MPO leaf epibiota recovery after disturbance
	1-10	2		Short-lived species recovery from episodic toxic pollution
	10-100	3		Long-lived species recovery from overfishing
	>100	4		*P. oceanica* above ground recovery after trawl damage
Certainty ***How well are the impacts documented?***	None	0		
	Low	1	Very little or no empirical work exists	
	Medium	2	Some empirical work exists or the expert has some personal experience	

	High	3	Body of empirical work exists or the expert has direct personal experience
	Very high	4	Extensive empirical work exists or the expert has extensive personal experience

c) Questionnaire

1. General information

Please provide the following information.

1. Name:

2. Affiliation:

3. How many years have you been working on *Posidonia oceanica* ecosystem:

4. Number of relevant publications including, peer reviewed papers, books, book chapters, official reports (grey literature):

5. Which part(s) of the food web has been the main focus of your research (please enter an **X** next to the trophic level you have been studying):

   P. oceanica above ground

   P. oceanica below ground

   MPO and UPO leaf and rhizomes epibiota

   Endofauna

   Benthic suspension and filter feeders (e.g. *Pinna nobilis*, sponges, *Sabella spallanzanii*)

   Mesograzers (e.g. Amphipoda, Isopoda, Tanaidacea, Gastropoda, Polychaeta)

   Macrograzers (e.g. *Sarpa salpa, Paracentrotus lividus*)

   Carnivores/ Omnivores (e.g. *Diplodus* spp. *Labrus* spp. *Sparus* spp.*, Symphodus* spp. *Hippocampus* spp.*, Echinaster sepositus, Asterina pacerii*)

   High level predators (e.g. adults of *Scorpaena* spp., *Conger conger, Serranus* spp.)

6. Which of the following threats and their impacts on *P. oceanica* ecosystem have you investigated (please enter an **X** next to the threats you have been studying)?

   Coastal development – permanent infrastructure

   Coastal development – small periodic interventions

   Industrial pollution

   Domestic pollution

Thermal pollution

Desalination

Agricultural runoff

Trawling

Fish farms

Anchoring

Mooring

Introduced species – macrophytes

Introduced species – herbivores

Introduced species – carnivores

Climate change – temperature rise

Climate change – acidification

Climate change – sea level rise

Climate change – native species change of abundance and/or distribution

7. At what scale are you working on *P. oceanica*? (please enter an **X** next to the appropriate scale)

   a. Plant Habitat Ecosystem

   b. <1 km 1-10 km 10-100km >100km >1000km

2. Vulnerability information. Please complete the tables having in mind a *Posidonia oceanica* meadow.

Please fill out the following tables based on your own experience and knowledge from literature review. If evaluation is not based on literature or on personal experience but on logical conclusions please insert a cross (+) next to the number (rank) you have inserted in the cell. Please insert only one rank value in each cell. Not determined (ND) is used when we know that there is no information relating a particular threat to a particular trophic group. If you do not know about the impact of a threat on a trophic group because we do not have information from literature, personal experience or cannot make logical assumptions, please leave the field in the table blank.

Table 1. Scale (m^2) of threat impact. What is the scale of the impact of the threat? Please enter in each cell one of the following numbers: 0= no threat, 1= less than 10 m^2, 2= 10 – 100 m^2, 3= 100 – 1000 m^2, 4= 1000 – 10000 m^2, 5=more than 10000 m^2 ND = Not determined. **Spatial scale is not the scale at which threats exist (most can be found almost everywhere). For example, a single pass of a demersal trawl may cover approximately 1–10 km^2, whereas demersal trawling overall affects 1000s of km^2 of continental shelf ecosystems each year. The vulnerability measure focuses on the first scale. For details on trophic component definition see point 5 at the beginning of this questionnaire.**

Threat / Trophic level	*P. oceanica* above ground	*P. oceanica* below ground	MPO & UPO leaf and rhizomes epibiota	Mesograzers	Macrograzers	Endofauna	Benthic suspension and filter feeders	Carnivores/ Omnivores	High level predators
Coastal Infrastructure (irreversible e.g. ports) on the site									
Coastal Infrastructure (irreversible e.g. ports) adjacent area									
Small periodic interventions (e.g. beach replenishment, dredging)									
Industrial pollution									
Domestic pollution									
Desalination									
Thermal pollution									

Agricultural runoff									
Fisheries (commercial and non-commercial)									
Trawling									
Fish farms on the site									
Fish farms on adjacent area									
Anchoring (anchor and anchor chain system)									
Mooring (fixed points)									
Introduced species - macrophytes									
Introduced species - herbivores									
Introduced species - carnivores									
Climate change – Temperature rise									
Climate change – Sea level rise									
Climate change - Acidification									
Climate change – Native species changes in distribution and abundance									

Table 2. Frequency. What is the frequency of the threat? Please enter in each cell one of the following numbers: 0=never, 1=rare, 2= occasional, 3= annual or regular, 4=permanent or persistent, ND = Not determined. **Frequency describes how often discrete threat events occur in a given ecosystem. For those threats that occur as discrete events, frequency represents how often new events occur, not duration of a single event. . For details on trophic component definition see point 5 at the beginning of this questionnaire.**

Threat / Trophic level	*P. oceanica* above ground	*P. oceanica* below ground	MPO & UPO leaf and rhizomes epibiota	Mesograzers	Macrograzers	Endofauna	Benthic suspension and filter feeders	Carnivores/ Omnivores	High level predators
Coastal Infrastructure (irreversible e.g. ports) on the site									
Coastal Infrastructure (irreversible e.g. ports) adjacent area									
Small periodic interventions (e.g. beach replenishment, dredging)									
Industrial pollution									
Domestic pollution									
Desalination									
Thermal pollution									
Agricultural runoff									
Fisheries (commercial and non-commercial)									
Trawling									
Fish farms on the site									
Fish farms on									

adjacent area									
Anchoring (anchor and anchor chain system)									
Mooring (fixed points)									
Introduced species - macrophytes									
Introduced species - herbivores									
Introduced species - carnivores									
Climate change – Temperature rise									
Climate change – Sea level rise									
Climate change - Acidification									
Climate change – Native species changes in distribution and abundance									

Table 3. Sensitivity to impact. How likely is that impact to affect the species in the affected trophic level? Please enter in each cell one of the following numbers: 0=no impact, 1=low (0-33% change in cover, density, abundance or community structure), 2= medium (33-66% change in cover, density, abundance or community structure), 3= high (66-100% change in cover, density, abundance or community structure), ND = Not determined. **For details on trophic level component definition see point 5 at the beginning of this questionnaire.**

Threat / Trophic level	*P. oceanica* above ground	*P. oceanica* below ground	MPO & UPO leaf and rhizomes epibiota	Mesograzers	Macrograzers	Endofauna	Benthic suspension and filter feeders	Carnivores/ Omnivores	High level predators
Coastal Infrastructure (irreversible e.g. ports) on the site									
Coastal Infrastructure (irreversible e.g. ports) adjacent area									
Small periodic interventions (e.g. beach replenishment, dredging)									
Industrial pollution									
Domestic pollution									
Desalination									
Thermal pollution									
Agricultural runoff									
Fisheries (commercial and non-commercial)									
Trawling									
Fish farms on the site									
Fish farms on adjacent area									
Anchoring									

(anchor and anchor chain system)									
Mooring (fixed points)									
Introduced species - macrophytes									
Introduced species - herbivores									
Introduced species - carnivores									
Climate change – Temperature rise									
Climate change – Sea level rise									
Climate change - Acidification									
Climate change – Native species changes in distribution and abundance									

Table 4. Recovery time (years). How long does it take to recover from exposure to the impact? Please enter in each cell one of the following numbers: 0=No impact, 1= less than a year, 2= between 1 and 10 years, 3= between 10 and 100 years, 4= more than 100 years, ND = Not determined. **Recovery time is the average time required for the affected trophic level to return to its pre-threat state. Because populations, communities, and ecosystems are dynamic in nature, they need not (and are unlikely to) return to their exact pre-threat condition to be deemed "recovered". For persistent threats we consider recovery time following removal of the threat. For details on trophic level component definition see point 5 at the beginning of this questionnaire.**

Threat / Trophic level	*P. oceanica* above ground	*P. oceanica* below ground	MPO & UPO leaf and rhizomes epibiota	Mesograzers	Macrograzers	Endofauna		Carnivores/ Omnivores	High level predators
Coastal Infrastructure (irreversible e.g. ports) on the site									
Coastal Infrastructure (irreversible e.g. ports) adjacent area									
Small periodic interventions (e.g. beach replenishment, dredging)									
Industrial pollution									
Domestic pollution									
Desalination									
Thermal pollution									
Agricultural runoff									
Fisheries (commercial and non-commercial)									
Trawling									
Fish farms on the site									
Fish farms on adjacent area									

Anchoring (anchor and anchor chain system)									
Mooring (fixed points)									
Introduced species - macrophytes									
Introduced species - herbivores									
Introduced species - carnivores									
Climate change – Temperature rise									
Climate change – Sea level rise									
Climate change - Acidification									
Climate change – Native species changes in distribution and abundance									

Table 5. Certainty. How well are the impacts documented? Please enter in each cell one of the following numbers: 0=none, 1= low, 2=medium, 3=high, 4= very high (refer to the vulnerability measure table at the end of the document). **For details on trophic level component definition see point 5 at the beginning of this questionnaire.**

Threat / Trophic level	*P. oceanica* above ground	*P. oceanica* below ground	MPO & UPO leaf and rhizomes epibiota	Mesograzers	Macrograzers	Endofauna	Benthic suspension and filter feeders	Carnivores/ Omnivores	High level predators
Coastal Infrastructure (irreversible e.g. ports) on the site									
Coastal Infrastructure (irreversible e.g. ports) adjacent area									
Small periodic interventions (e.g. beach replenishment, dredging)									
Industrial pollution									
Domestic pollution									
Desalination									
Thermal pollution									
Agricultural runoff									
Fisheries (commercial and non-commercial)									
Trawling									
Fish farms on the site									
Fish farms on adjacent area									
Anchoring (anchor and									

anchor chain system)									
Mooring (fixed points)									
Introduced species - macrophytes									
Introduced species - herbivores									
Introduced species - carnivores									
Climate change – Temperature rise									
Climate change – Sea level rise									
Climate change - Acidification									
Climate change – Native species changes in distribution and abundance									

d) Literature review on human threats' impacts on *Posidonia oceanica* food components

Table S1.2: Available literature on impacts of threats on food web components. Numbers correspond to the references listed below.

Threat / Trophic level	*P. oceanica* above ground	*P. oceanica* below ground	MPO & UPO leaf and rhizomes epibiota	Mesograzers	Macrograzers	Endofauna/ Detritus feeders	Benthic suspension and filter feeders	Carnivores/ Omnivores	High level predators
Coastal Infrastructure (irreversible e.g. ports) on the site	7, 8, 18, 24, 45	7, 8, 18, 24, 45							
Coastal Infrastructure (irreversible e.g. ports) adjacent area	7, 8, 18, 24, 45, 41	7, 8, 18, 24, 45, 41							
Small periodic interventions (e.g. beach replenishment, dredging)	3, 7, 8, 18, 23, 27	3, 7, 8, 18, 23							
Industrial pollution	4, 7, 8, 25, 26, 50	4, 7, 8, 25, 26, 50							
Domestic pollution	4, 7, 8, 10, 11, 18, 50, 52	4, 7, 8, 10, 18, 50, 52	10, 11, 18, 42	11, 42					
Desalination	7, 18, 29	7, 18, 29	29						
Thermal pollution	30, 43, 48	43							
Agricultural runoff	7, 18	7, 18	18						
Fisheries (commercial and non-commercial)								9	9
Trawling	7, 8, 18, 33, 39	7, 8, 18, 33, 39		59, 60	59	5, 59	59	59	59
Fish farms on the site	2, 7, 8, 13, 14, 18, 20, 34, 20, 57	2, 7, 8, 14, 18, 19, 21, 34, 57	13, 14, 18, 34, 20, 57	1, 34, 19	1, 19	1, 34			
Fish farms on	2, 7, 8, 13,	2, 7, 8, 14,	12, 14, 18, 34,	1, 34, 19	1, 19,	1, 34			

adjacent area	14, 18, 20, 34, 19, 57, 58	18, 33, 19, 57, 58	19, 57, 58						
Anchoring (anchor and anchor chain system)	7, 8, 12, 18, 28, 44, 47	7, 8, 12, 18, 28, 44, 47							
Mooring (fixed points)	7, 8, 18	7, 8, 18							
Introduced species - macrophytes	5, 7, 8, 16,17, 18, 22, 35, 36, 38, 39, 40, 46, 49, 51, 55	7, 8, 16, 17,18, 39, 40, 46, 49, 51, 55	15, 54, 56						
Introduced species - herbivores	51						51		
Introduced species - carnivores								37, 51	51
Climate change – Temperature rise	7, 18, 43, 48, 49, 51	7, 18, 47, 49, 51							
Climate change – Sea level rise	7, 51	7, 51							
Climate change - Acidification	51		51	31, 51	51	51			
Climate change – Native species changes in distribution and abundance								51	51

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e) Threats' definitions

Coastal Infrastructure on the site: Direct impacts from large-scale permanent coastal constructions, such as ports, or reclamation for coastal development at the location where the construction takes place.

Coastal Infrastructure in adjacent area: Indirect impacts from the coastal constructions e.g., change in sedimentation flow, water movement in adjacent areas.

Periodic interventions: Impacts from non-permanent coastal actions, such as small beach nourishment or dead *Posidonia* leaves (banquette) removal.

Trawling: Impacts from trawling activities, producing mechanical damage (e.g., shoots uproot, matte erosion) and hypersedimentation.

Fishing (other than trawling): Impacts from fishing practices both commercial and non-commercial which have a low mechanical impact because they act as passive fishing gears.

Fish farms on the site: Direct impacts of fish farms and aquaculture, such as increased nutrients, hypersendimentation, and limited light penetration, at the location where the farm is established, at scale of 100's m.

Fish farms in adjacent area: Indirect impacts of the fish farms/aquacultures in adjacent areas because dilution of pollutants and dispersion at scale of 1000's m.

Industrial pollution: Impacts from industrial discharge or sewage, which can contain toxic chemical product in addition to organic and nutrient enrichment.

Domestic pollution: Impacts from urban sewage, wastewater which can contain mainly organic matter, with some kind of domestic chemical pollution.

Thermal pollution: Impacts from power plants discharges because the use of water as refrigerate, increasing average value of water temperature in the environment.

Desalination: Impacts from the waste water from the inverse osmosis, which produce a high salinity discharge of brine water.

Agricultural runoff: Impacts from river or ground water because agricultural activities, such as nutrient enrichment, herbicides, and modified sediment dynamic.

Anchoring: Impacts from mechanical damage caused by anchor and anchor chain.

Mooring (fixed points): Impacts from mechanical damage caused by chains of fixed mooring installations.

Introduced species – macrophytes: Impacts from invasive alien macrophyte species.

Introduced species – herbivores: Impacts from invasive alien low trophic level (<3) species.

Introduced species – carnivores: Impacts from invasive alien high trophic level (> 3) species.

Climate change – Temperature rise: Impacts from sea water temperature rise due to climate change (including extreme events).

Climate change – Acidification: Impacts from sea water pH decrease and carbonate chemistry alteration due to climate change.

Climate change – Sea level rise: Impacts from sea level rise due to climate change.

Climate change – Native species changes: Impacts from native species biogeographic changes and relative dominance due to climate change.

Table S1.3: Stressors caused by each threat.

Threat	Stressors
Coastal Infrastructure on the site	Direct burial
Coastal Infrastructure in adjacent area	Increase in turbidity, upstream hypersedimentation and downstream erosion with modifying effects of coastal drift and pollution
Periodic interventions	Direct burial, hypersedimentation and downstream erosion with modifying effects of coastal drift
Trawling	Mechanical damage (uproot), sediment erosion
Fishing other than trawling	Direct removal of higher level food web components

Fish farms on site	Pollution and eutrophication, turbidity, reduction in light intensity, hypersedimentation, sediment anoxia
Fish farms in adjacent area	Eutrophication, turbidity, hypersedimentation
Industrial pollution	Pollution, turbidity, hypersedimentation, eutrophication
Domestic pollution	Pollution, turbidity, hypersedimentation, eutrophication
Thermal pollution	Turbidity, increased temperature
Desalination	Increased salinity, salinity variability
Agricultural runoff	Pollution and eutrophication, turbidity, hypersedimentation
Anchoring	Mechanical damage, changes in sediments biogeochemistry, erosion
Mooring	Mechanical damage, changes in sediments biogeochemistry, erosion
Introduced species – macrophytes	Competition, direct shading
Introduced species – herbivores	Predation (overgrazing), competition
Introduced species – carnivores	Predation, competition
Climate change – temperature rise	Increased sea temperature, increased CO_2 concentration, increased ultraviolet irradiance
Climate change – acidification	Increased CO_2 concentration, carbonate chemistry and pH alteration
Climate change - sea level rise	Shoreline erosion, increased wave action
Climate change – native species changes	Predation, competition

Appendix S2: Description of the conceptual *Posidonia oceanica* food web

Organisms found in *Posidonia oceanica* meadows are bound together by intricate trophic interactions forming a complex food web (Fig. 2 in manuscript).

Complexity starts at the base of this food web that features multiple primary producers and organic matter sources (green boxes on Fig. 2). *P. oceanica* itself is the main producer of the system in terms of biomass. Aboveground (**leaves**) and belowground (**roots and rhizomes**) tissues of the seagrass have different physical and chemical features, and consequently different potential roles in the food web. They can therefore be seen as two different compartments (Fig. 2). Although biomass of available seagrass tissues is very high, few direct grazers are able to exploit them efficiently. The reasons for this limited consumption include poor nutritional value, low palatability (abundance of lignin or cellulosic compounds) and chemical defense through polyphenolic compounds (Vizzini, 2009).

Due to its large size and long life span, the epibiotic cover of *P. oceanica* is one of the most diverse and abundant of all seagrasses (Hemminga & Duarte, 2000; Mazzella *et al.*, 1989). Many multi- and unicellular photosynthetic organisms (**MPO** and **UPO,** respectively) grow on its **leaves**. **Rhizomes** also bear **MPO**'s. Since the habitat they offer is different from leaves, in terms of structure and microclimatic conditions, rhizome and leaf MPO communities are different (Buia *et al.*, 2000), and are not necessarily consumed by the same organisms (Michel *et al.*, 2014). They accordingly constitute two different compartments of our model (Fig. 2). Nutritional value of plant epibiota is typically higher than the one of seagrass tissues. Their palatability is also better, since they usually contain less structural compounds (*e.g.* Raven *et al.*, 2002). In addition, the diversity of epiphytic structures and functions makes them adequate for different feeding techniques and food intake mechanisms of consumers (Buia *et al.*, 2000). As a result, photosynthetic epibiota support diverse communities.

Most of *P. oceanica* tissues are not consumed while alive, and instead enter a **detritus** pool along with the epibiota they bear. All living organisms contribute to detritus, but the greatest contribution comes from primary producers. Therefore only this connection was depicted in Figure 1, while connections with other organisms are not presented for the sake of readability. This pool, often called "*Posidonia* litter" is a heterogeneous compartment that also contains remains of organisms originating from adjacent habitats (*e.g.* algae from surrounding rocky shores). Detritus can be exploited by various consumers, but can also be exported to the terrestrial realm (**beach wrack, or banquette**) or to **deeper zones**. Finally, it can be buried in the **matte** (Cebrian & Duarte, 2001; Mateo & Romero, 1997). This terrace-like formation is typical of *P. oceanica* meadows. It is formed by several strata of intertwined rhizomes and roots, as well as vast amounts of trapped sediment, and it constitutes an important carbon sink (Boudouresque *et al.*, 2012; Gobert *et al.*, 2006). Besides these organic matter sources that are located inside the meadow, *P. oceanica*-associated food webs also receive inputs from production that takes place outside the seagrass system itself (limits of this system are pictured on Fig. 2 by the green dashed line). This is notably the case of **phytoplankton** and **suspended particulate organic matter** that can sink from the water column to the *Posidonia* meadow (Velimirov, 1987) and be retained because of the reduced hydrodynamism due to the canopy modification of the boundary layer (Gacia & Duarte, 2001).

Primary consumers (purple boxes on Fig. 2) have a central role in seagrass-associated food webs (Buia *et al.*, 2000). In the Mediterranean Sea, large herbivores such as sea turtles are relatively rare. Their overall grazing pressure at the scale of the whole basin is therefore likely low. Other herbivores mostly fall into two categories. **Mesograzers** were initially described as small invertebrate grazers whose size exceeds the one of a typical copepod, but is smaller than 2.5 cm, and who live permanently in the same habitat they exploit (Brawley, 1992). They include peracarids (e.g., amphipods, tanaids, isopods) and decapod crustaceans, gastropod mollusks and polychaetes (Gambi *et al.*, 1992; Scipione, 2013).

Some species can occasionally consume tissues of their host plant. However, actual contribution of seagrass leaves to their diet is typically low or nil, and mesograzers primarily rely on seagrass epibiota, such as benthic diatoms and macroalgae, for their subsistence (Lepoint *et al.*, 2000; Michel *et al.*, 2014; Vizzini, 2009). These vagile organisms can move along the different strata of the meadow, and therefore consume epibiota from leaves and/or rhizomes (Michel *et al.*, 2014). Moreover, some of them are not strict herbivores, but also feed on the sessile epifauna growing on *P. oceanica* (Lepoint *et al*., 2000), that is dominated by bryozoans and hydrozoans (purple box on Fig. 2). **Macrograzers** are of larger size than the former category. In *P. oceanica* meadows, they are mostly represented by the fish *Sarpa salpa* and the sea urchin *Paracentrotus lividus*. These two organisms are responsible for most of the direct seagrass herbivory (Tomas *et al.*, 2005b; Vizzini, 2009). While ingesting seagrass leaves, they also consume the photosynthetic epibiota and sessile epifauna that they bear. Albeit it is still a matter open to discussion, the percentage of organic matter they derive from these food sources, which are more easily digestible and have higher nutritional value than the seagrass itself, seems significant (Havelange *et al.*, 1997; Prado *et al.*, 2007; Tomas *et al.*, 2005a).

Epifaunal filter and **suspension feeders** are sessile organisms living inside the meadow, between the shoots, but fixed directly on the substrate rather than on the seagrass. This compartment contains mainly sponges, sessile polychaetes, bryozoans, tunicates, and also protected bivalves such as *Pinna nobilis*. Like ***P. oceanica*** **sessile epifauna** (orange box on Fig. 2), they primarily rely on phytoplankton, zooplankton and SPOM for their organic matter intakes.

As mentioned earlier, seagrass tissues predominantly enter the food webs under detrital form (Vizzini, 2009). Detritus is readily colonized by a number of micro-organisms, including **bacteria**, **archaea**, **fungi** (modern meaning) and **heterotrophic stramenopiles** (the BAFHS compartment). Heterotrophic stramenopiles of the BAFHS compartment mainly belong to oomycota and labyrinthulomycota. Activity of these organisms cause degradation of detritus.

Detritus-feeders consume ('licking') BAFHS, rather than proper detritus. All organisms contribute to the production of DOC (**Dissolved Organic Carbon**) but, for reasons of readability, arrows were not inserted in the diagram. Although DOC belongs to the detritus pool, for the ease of the food web representation, it was separated from the detritus compartment which represents particulate organic carbon (Velimirov, 1991). DOC is consumed by a number of heterotrophic prokaryotes which are in turn consumed by unicellular eukaryotic predators, mostly **flagellated** heterotrophic stramenopiles. These flagellates are in turn eaten by larger micro-organisms such as **ciliates** (Azam *et al.*, 1983; Bratbak *et al.*, 1994).

A wide assemblage of **detritus feeders** ingest *P. oceanica* litter. It includes gastropods, amphipod, isopod and decapod crustaceans, as well as echinoid, ophiuroid and holothuroid echinoderms (Buia *et al.*, 2000; Mazzella *et al.*, 1992; Vizzini, 2009). The unique guild of sheath borers, represented by specialized polychaetes (Eunicidae) and the isopod *Limnoria mazzella*, should also be included in the detritus feeders (Guidetti *et al.*, 1997; Gambi *et al.*, 2003). The interest of *P. oceanica* litter as a food source is questionable. Since structural carbohydrates are refractory to chemical degradation, appreciable amounts remain in the litter fragments. Nutritional quality is even worse than the one of living tissues, as most labile organic C, N and P is lost by remobilization from the senescent leaves or by decomposition after tissue death (Romero *et al.*, 1992). It is commonly accepted that detritivores feeding on litter rely on micro-organisms colonizing detritus (BAFHS, flagellates, ciliates) to achieve nutritional balance (Vizzini, 2009). Moreover, dead *P. oceanica* material is not their only food source, as they also consume multicellular photosynthetic organisms present on dead rhizomes and leaf fragments (Lepoint *et al.*, 2006). Trophic activity of detritus feeders as well as water movements cause mechanical breakdown (fragmentation) of detrital items into smaller particles that can be buried in the sediment underlying the meadow, and that on surface is consumed by large holoturians (*Holoturia* spp.). The **infaunal invertebrates,** known as **endofauna**, include mainly sub-surface detritus feeders that dwell in the matte (notably peracarid and decapod crustaceans, mollusks, and polychaetes; see Borg *et al.*, 2006) and feed on finer detritus, as well as on seston that sank to the bottom.

Many **secondary consumers** (light blue box on Fig. 2) also live in *P. oceanica* meadows (Mazzella *et al.*, 1992). They include meso-carnivores (mainly Syllidae polychaetes, opistobranch mollusks, and decapod crustaceans) that rely on the sessile epibiota, and carnivores as decapod crustaceans (various species of crabs, but also shrimps, hermit crabs, and squat lobsters), cephalopods (*Sepia* spp., *Octopus* spp.) and gastropod mollusks (e.g., *Hexaplex trunculus*), echinoderms (*Echinaster sepositus, Asterina* spp., *Marthasteria glacialis*) and fishes (*Diplodus* spp., *Labrus* spp., *Symphodus* spp., etc.). A large number of feeding strategies exist among these organisms, which predominantly feed on primary consumers mentioned above. Some of them occasionally consume photosynthetic epibiota and/or seagrass tissues, therefore displaying a certain degree of omnivory (Lepoint *et al.*, 2000; Vizzini *et al.*, 2002).

Besides these organisms, some tertiary or **higher level** consumers (dark blue box on Fig. 2) are strict **predators** that feed only on secondary consumers. This is the case of some fishes such as *Scorpaena* spp. or *Conger conger*, whose diet is exclusively piscivorous (Boudouresque *et al.*, 2012). Many of these secondary or higher level consumers are highly motile organisms, such as fish or large invertebrates. While some of them spend most of their lives inside the *P. oceanica* meadow, others move to other neighboring ecosystems. These migrations can be related to ontogenetic changes. Some fishes can indeed spend their larval and/or juvenile phases among seagrass meadows while adults live in pelagic zones (*e.g. Sardinella aurita* or *Engraulis encrasicolus*; del Pilar Ruso & Bayle-Sempere, 2006) or rocky habitats (*e.g. Epinephelus marginatus*; Harmelin & Harmelin-Vivien, 1999). There can also be movements of adult animals: fishes of the genus *Diplodus* are mostly benthic feeders, but can exploit items originating from the water column (Pinnegar & Polunin, 2000). Finally, regular migrations also occur. For example, the fish *Chromis chromis* spends nighttime resting in seagrass meadows, but actively hunts zooplankton during the day

(Boudouresque *et al.*, 2012). In all cases, these animal movements cause cross-ecosystem transfers of organic matter. These transfers can go in both directions. For example, while outside the *P. oceanica* system, typical residents of meadows could be eaten by predators that do not belong to the seagrass system. Conversely, pelagic fish venturing inside the meadow could be preyed upon by predatory organisms that spend most of their life in it. The net result of these linkages in terms of input or output of biomass for the *P. oceanica* system is currently hard to assess due to the lack of adequate data.

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Appendix S3: Uncertainty related to each food web component/threat combination.

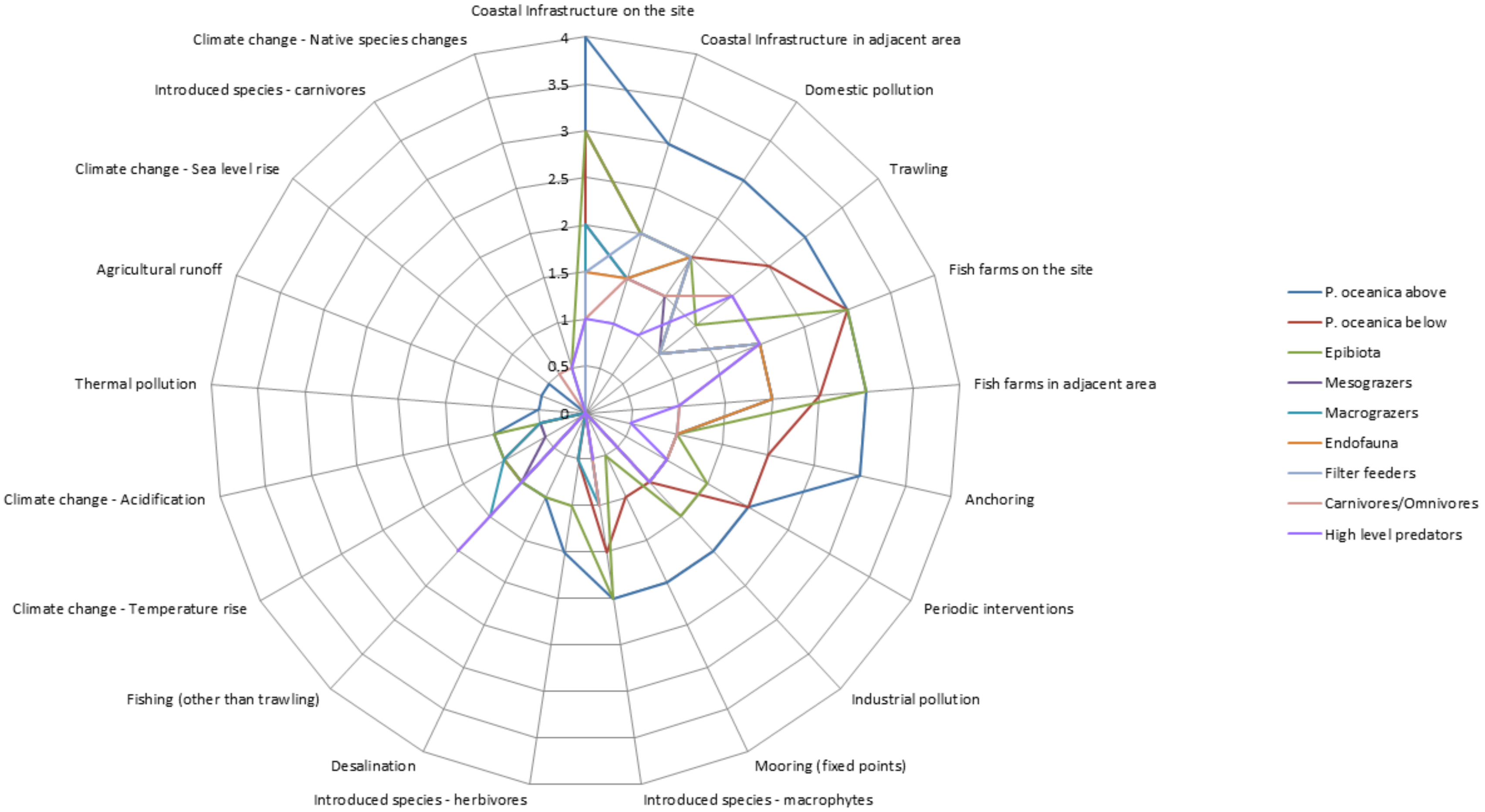

Figure S3.1: Radar chart presenting the relative availability of data for each food web component (color lines) and threat (spokes) combination.