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Assessing discard consumption dynamic in shallow coastal environment using underwater video

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Abstract:

Food webs are typically studied with respect to predator-prey interactions while often neglecting to address the role or importance of scavenging (i.e. carrion consumption) on their structure and functioning. In some environmental contexts, scavenging can play a key role in supporting populations and communities as exemplified by seabirds feeding on fisheries discards. Yet, a substantial part of fisheries discards sinks in the ocean where the range of consumers is most likely underestimated, owing to a lack of comprehensive understanding of the scavenging ability of marine fauna and local-scale empirical studies. Here, we deployed baited remote underwater video surveys (BRUVs) using discarded fish as baits to study the taxonomic richness of consumers, their interactions and consumption dynamic of discards in shallow coastal fishing grounds subject to discarding (Bay of Bourgneuf, North East Atlantic, France). We show that discards attract and are consumed by a wide taxonomic and trophic diversity of species. Interestingly, only one species observed is considered an obligate scavenger, while scavenging is little known or considered anecdotal in most other identified taxa. Analysis of consumption dynamic and interactions around discards revealed intra and interspecific competition among discard consumers as well as successions between consumers involved in predator-prey interactions. Data also suggests that decapods may facilitate discard consumption by non-piscivorous fish by generating scraps during consumption. We argue that underwater video surveys provide a valuable tool to better assess the occurrence and extent of facultative scavenging behaviors within marine communities and understand its role in food web dynamic.

1. Introduction

Food webs are typically studied with respect to predator-prey interactions while often neglecting to address the role or importance of scavenging (i.e. the consumption of carrion, or dead animals, that the consumer has not killed itself) on their structure or functioning (Beasley et al., 2015; Depestele et al., 2019). In some environmental contexts, scavenging can play a key role in supporting populations and communities, and be linked to human activities, as exemplified by seabirds feeding on fisheries discards (e.g. Garthe et al. 1996; Votier et al. 2004; Sherley et al. 2019). Fisheries discards correspond to unwanted catches (or bycatches) that are immediately returned to the sea, either dead or alive. Together with offal (discharge resulting from the processing of some target species onboard, e.g. guts, head, fins), they correspond to fisheries waste that may reintegrate marine food webs and support various marine fauna in sometimes neglected or underassessed ways (Laptikhovsky et al., 2006; Lejeune et al., 2022b). Indeed, a substantial part of fisheries waste is not directly consumed by above surface scavengers, but sinks through the water column to become potential food sources for pelagic, demersal and finally benthic organisms (Depestele et al., 2016; Oro et al., 2013). Yet, their consumption is considered to be underestimated in marine ecosystems, owing to a lack of comprehensive understanding of the scavenging ability of marine fauna and local scale empirical studies (Depestele et al., 2019; Guillen et al., 2018). In particular, little information is available about how species interactions may structure scavenger communities either via antagonistic behaviors (e.g. limiting the access to discards Davenport et al., 2016) or positive interactions (e.g. gaining access to discards by relying on other better equipped species such as crabs for dismantling them first; Jenkins et al., 2004).

Two types of scavengers can be distinguished: obligate scavengers (e.g. hagfish) that rely on carrion for survival or reproduction and facultative scavengers (e.g. crustaceans, echinoderms, fish) feeding on dead animals but which do not depend solely on carrion for their

survival or reproduction (Beasley et al., 2015). While the first category is restrictive and relatively well studied, studying facultative scavenging behaviors in marine fauna is a difficult task. Indeed, carrion, whether naturally occurring or linked to fishing (e.g. fisheries discards or marine fauna damaged by towed gear) are typically considered scarce, unpredictable and potentially quickly assimilated in marine environments (Davenport et al., 2016; Depestele et al., 2019). Moreover, diet assessment based on gut content analysis cannot ascertain whether ingested items were alive preys or carrion. Consequently, one may have to rely on other information such as consumers known diet, trophic traits (e.g. trophic level, trophic guild) and the importance of local discarding activity to evaluate whether specific prey ingestions likely resulted from predation on live prey or scavenging on discards (Lejeune et al., 2022b). In addition, it is not clear whether obligate scavengers or piscivorous species would necessarily be the first to detect and consume carrion or whether other species seemingly less adapted to consume this type of resource may more generally be able to benefit from it. One way to assess whether species are attracted and able to consume carrion (i.e. depicting scavenging behavior) is to rely on baited remote underwater videos (BRUV) using carrion as baits (e.g. Jenkins et al. 2004; Davenport et al. 2016). This is considered one of the only technique allowing direct observation of discard consumption, while also allowing to study its dynamic, including detection time, chronology of arrival of different groups and species interaction around discards to empirically determine the scavenging abilities of diverse marine fauna. Better understand the process of reintegration of discards within marine food webs is a timely issue since multiple countries around the world (e.g. the European Union, Norway, Chile, New Zealand) are currently aiming to reduce discarding practices (Guillen et al., 2018).

Here, we aimed to obtain direct evidence of species attracted and consuming discards, as well as describe discard consumption dynamic (consumers detection time, chronological order of arrival and associations) and characterize consumers behavioral interactions around

discards that might play a role in consumption dynamic. To this end, we conducted BRUV surveys in a shallow coastal fishing ground subject to discarding activity (Bay of Bourgneuf, France, North East Atlantic). We hypothesized that (1) discards would not only attract obligate scavengers, but also a wide range of opportunistic species that are not typically considered as scavengers, (2) antagonistic interactions (competition or predation) may play a role in structuring discard consumption dynamic and (3) species which may be deemed unable to feed upon discarded fish according to their trophic morphology or known ecology may benefit from the presence of better equipped scavengers allowing them to exploit discards (e.g. presence of crabs dismantling and dispersing discards).

2. Material and methods

2.1 Study site

The study took place in the Bay of Bourgneuf (Bay of Biscay, France, Northeast Atlantic; 2.30°W 47.05°N). The bay is shallow (from 0 to 34 m depth) and covers a relatively small area (320 km²), but is diverse in terms of substrate types (i.e composed of a variety of patchy rocky, sandy and muddy bottoms) and species occurrence (Gauduchon et al., 2020). It has long been exploited by fisheries and subject to discarding practices (Cornou et al., 2021), which makes it an ideal area to study potential discard consumers and to describe intra and inter specific interactions around discards. The climate is temperate and oceanic with a mean daily air temperature ranging from 4 °C in January to 23 °C in August (Morfin et al., 2019). In July-August, averaged daily water temperature is 15 °C (min-max range = 13 – 26 °C).

2.2 Video deployment and acquisition

We monitored the consumption of discards by local marine fauna during daylight using baited remote underwater video systems (BRUVs) set on the sea bed within a 2 km radius in the bay of Bourgneuf and at depth ranging between 5 and 12m, between July and August of 2019 and 2020. BRUVs consisted in a camera (GoPro Hero 7) fixed to a cage or a tripod, orientated towards the seafloor and pointing towards a bait (i.e. discarded fish carcass) (Figure A.1). One to three dead fish from a single species were fixed within the field of the camera with spikes or strings. Dead fish used were collected from local discarding activity and corresponded to some of the species most commonly discarded in the area: horse mackerel (*Trachurus trachurus*), black seabream (*Spondyllosoma cantharus*), gurnards (*Eutrigla gurnardus* or *Chelidonichthys cuculus*), mackerel (*Scomber scombrus*), whiting (*Merlangius merlangus*), hake (*Merluccius merluccius*), and pout (*Trisopterus luscus*).

2.3 Data collection

A total of 31 videos ranging from 17 min 34 s to 5 h 14 min 34 s were analyzed over the study period (Table 1). Each video sequence begins once the BRUV is settled on the bottom and ends when the discard is no longer visible (consumed or dragged outside of the camera's view) or the memory storage is full. For each video sequence, we noted the taxonomic identity of each individual consumer, the start of consumption time (i.e. when the individual touches and consumes the discard or parts of it that were previously scattered around the BRUV by other consumers), the end of consumption time (i.e. leaving) and occurrences of intra or interspecific behavioral interactions happening within the field of the camera. It is worth noting that contact with the discard could only be acknowledged when occurring above it, since any contact happening below would be out of the camera's field. All consumers were identified to the

lowest taxonomic level possible based on morphological characteristics, following Martin (2011) for invertebrates and Froese and Pauly (2021) for fish.

Table 1: Summary of videos data. ID = video ID. Discards = number of individual baits used. Fixation = camera's fixation system. Seafloor contact: 1 = direct contact between the discard and the seafloor, 0 = no contact. Algae: 1 = presence of algae, 0 = no algae. Visibility = visibility score (1 = correct, 2 = medium and 3 = low).

ID	Date	Discards	Discard species	State of the discard	Fixation	Seafloor contact	Granulometry	Algae	Visibility	Video length (minutes)	Taxonomic richness
1	19-08-20	1	Black seabream	Good	Cage	1	Cobble	1	3	59.95	1
2	09-08-20	1	Mackerel	Good	Cage	0	Cobble	1	2	75.02	4
3	12-08-20	1	Mackerel	Good	Cage	1	Gravel	0	2	163.62	5
4	18-08-20	1	Whiting	Good	Cage	0	Cobble	1	2	84.32	2
5	09-08-20	2	Hake	Deteriorated	Cage	0	Cobble	1	1	74.73	3
6	18-08-20	1	Hake	Deteriorated	Cage	0	Sand	0	1	74.9	2
7	11-08-20	1	Horse mackerel	Good	Cage	0	Cobble	1	2	126	3
8	15-08-20	1	Horse mackerel	Good	Cage	1	Gravel	1	2	115.73	4
9	11-08-20	1	Pout	Good	Cage	1	Sand	0	2	132.53	3
10	11-08-20	2	Pout	Good	Cage	1	Sand	0	2	182.28	5
11	18-08-20	3	Gurnard	Good	Cage	1	Sand	0	2	267.92	7
12	15-08-20	2	Horse mackerel	Good	Cage	1	Sand	1	2	25.58	1
13	11-08-20	1	Horse mackerel	Good	Cage	0	Gravel	1	2	178.82	4
14	18-08-20	2	Hake	Good	Cage	0	Cobble	1	1	167.95	1
15	19-08-20	2	Gurnard	Good	Cage	1	Sand	1	3	129.98	1
16	19-08-20	3	Hake	Good	Cage	0	Sand	1	2	314.57	5
17	19-08-20	3	Black seabream	Good	Cage	0	Sand	1	2	186.87	3
18	18-08-20	1	Whiting	Good	Cage	0	Sand	1	2	102.13	2
19	08-08-19	1	Horse mackerel	Good	Tripod	0	Cobble	1	2	80.1	3
20	22-08-19	1	Horse mackerel	Good	Cage	1	NA	1	2	149.73	5
21	26-08-19	1	Horse mackerel	Good	Tripod	0	Cobble	1	3	135.1	4
22	10-09-19	1	Horse mackerel	Good	Cage	1	Sand	0	3	130.18	3
23	21-08-19	1	Horse mackerel	Good	Cage	1	Gravel	1	2	62.38	3
24	21-08-19	1	Gurnard	Good	Tripod	0	Sand	1	2	192.87	3
25	22-08-19	1	Gurnard	Good	Tripod	0	Sand	1	1	150.3	1
26	05-09-19	1	Mackerel	Good	Cage	1	Cobble	1	1	29.57	4
27	06-09-19	1	Mackerel	Good	Cage	1	Gravel	1	2	17.57	1
28	08-09-19	1	Mackerel	Deteriorated	Tripod	0	Cobble	1	3	242.07	3
29	19-08-19	1	Pout	Good	Tripod	0	Gravel	1	1	215.22	2
30	26-08-19	1	Pout	Deteriorated	Cage	1	Gravel	1	1	39.38	3
31	10-09-19	1	Pout	Good	Tripod	0	Cobble	0	3	98.65	3

2.4 Description of discard consumers taxonomic richness

We characterized consumer taxa occurrence and taxonomic richness observed across BRUVs to obtain a view of the diversity of potential discard consumers in the Bay of Bourgneuf. Taxonomic richness was assessed by counting the total number of different consumer taxa present in each video sequence. We used a multiple regression approach with model selection and averaging based on the AICc ($\Delta < 2$) in the R package MuMIn (Bartoń, 2016) in R version 3.1.0 (R Core Team, 2021) to explore the potential influence of experimental and environmental variables (categorical and continuous) on consumers taxonomic richness prior to further data analysis. Independent experimental and environmental variables tested were : video length, year, species used as discard, number of discards (unique or multiple), fixation system (cage or tripod), presence/absence of algae, visibility (score : “1” = correct visibility, “2” = presence of elements (e.g. algae) partly blocking the view of the camera from time to time, and “3” = turbid water or algae significantly blocking the view of the camera), condition of the discard at the beginning of the video (good or deteriorated [i.e. presence of sores on the body]), granulometry (“pebbles” for particles larger than 75 mm in diameter; “gravels” for particles size between 4.75 and 75 mm and “sands” for particle below 4.75 mm) and contact of the discard with the seafloor.

2.5 Discard consumption dynamic and patterns of consumer taxa associations

We described the speed of detection and chronological order of arrival of the different discard consumer taxa to evaluate whether some groups would arrive significantly faster than others (e.g. obligate scavengers, piscivorous consumers) and whether there was a pattern in the chronological order of arrival of the different consumer groups across BRUVs. Detection time and chronological order of arrival were determined based on the time of arrival of the first

individual and departure of the last individual of each discard consumer taxon within each video sequence (i.e. together constituting the window of consumption time of each consumer taxon). In these analyses, consumers were grouped in six groups characterized by different morphologies, locomotion mode and trophic ecology: Piscivorous teleost fish (European conger eel), non-piscivorous teleost fish, crabs (also including hermit and spider crabs), shrimps, gastropod (netted dog-whelk) and starfish. Teleost fish were split piscivorous and non-piscivorous species (Thompson et al., 2020) following the hypothesis that piscivorous fish may behave differently than non-piscivorous fish in the face of discarded fish). Differences in detection time among groups of consumers were tested using a one-way PERMANOVA with Euclidean distances and 9999 permutations of residuals using a Monte Carlo resampling procedure (i.e. the equivalent of a non-parametric ANOVA), followed by post hoc pairwise tests between the different consumer groups using the same procedure. These tests were conducted in PRIMER version 7 software (Clarke and Gorley, 2006) and the PERMANOVA+ add-in (Anderson et al., 2008). Chronological arrival data were analyzed by calculating the proportion of each taxon occupying each position (e.g. first, second, third) in the chronological order of arrival of the different consumers over the entire video set.

Finally, we tested for overall patterns of discard consumer taxa associations (positive, negative or random) across all videos following a probabilistic model approach (Veech, 2013) using the cooccur R package (Griffith et al., 2016). This approach uses presence-absence data from each video sequence to calculate an expected frequency of co-occurrence between taxa pairs following the hypothesis that they are distributed independently of one another across videos. Then, the model calculates the probability that the observed co-occurrence frequency is greater than the expected frequency (a positive co-occurrence association), less than the expected frequency (negative association), or random, using a α threshold of 0.05 to characterize significant differences (p-value < 0.05).

2.6 Behavioral interactions among discard consumers

To gain insight into the potential role of intra and inter specific interactions in discard consumption dynamic, we quantified the occurrence of four types of behavioral interactions as they occurred along videos: “succession events”, “intra- and interspecific repulsions” and “positive interactions”. Characterization of these interactions are based on successions and overlaps between windows of consumption time of different consumers (i.e. from the moment an individual starts consuming the discard until the moment it leaves). In the case of fish consuming parts of the discard scattered around by other consumers, the end of consumption window was considered to be the moment when the fish got out of the camera’s field. Cases where some individuals would leave for a short time but stay within the camera’s field and come back to consume were considered as a single consumption event. If multiple individuals of the same species were indistinguishable, consumption windows were considered at the taxon level, from the first individual arrival until the moment they all left. “Succession events” were considered whenever the consumption window of two different taxa followed each other without any visible antagonistic interaction and within a 15 min timeframe. The occurrence of “intra- and interspecific repulsions” were characterized whenever a consumer left in response to the arrival of another consumer from the same or different taxon, respectively, while clearly displaying antagonistic behaviors such as hunting, pushing or escaping. Finally, “positive interactions” were considered whenever the prior presence of one consumer taxon seemed to favor consumption by another (e.g. promoting access to the discard). In addition, we specifically recorded *Nassarius reticulatus* abundance every 10 min along each video sequence to study its variation in relation to the presence of other potentially predatory species, since it was the only obligate scavenger and the most abundant species observed. Negative behavioral interactions among discard consumers were visualized using quantitative interaction networks

by linking repulsed species to their aggressors and quantifying repulsion occurrences across all videos in the Bipartite R package (Dormann et al., 2008).

3. Results

3.1 Discard consumers' taxonomic richness and influencing factors

18 different consumer taxa were observed in the 31 underwater videos (Figure 1; Figure A.2). Consumers belonged to six groups characterized by different morphologies, locomotion mode and trophic ecology: Piscivorous teleost fish, non-piscivorous teleost fish, crabs, shrimps, gastropods and starfish. There was only one gastropod species: the netted dog whelk (*Nassarius reticulatus*), which represented the most common taxon, occurring in more than 60% of the videos. Shrimps were present in 42% of the videos and ranked at the infra-order level (Caridea). Among crabs, four different taxa were identified at the species level: the velvet crab (*Necora puber*), the common spider crab (*Maja brachydactyla*), the edible crab (*Cancer pagurus*) and the European green crab (*Carcinus maenas*), which occurred in 35%, 26%, 3% and 3% of the videos respectively, and two at genus level: spider crabs belonging to (*Macropodia* sp.) and hermit crabs (*Pagurus* sp.), respectively in 6% and 3% of the videos. 20% of the videos also contained crabs that could only be ranked at the infra-order level (Brachyura). There was only one piscivorous teleost fish: the European Conger (*Conger conger*), which occurred in 16% of the videos. Among non-piscivorous teleost fish, two were identified at the species level: the common pout *Trisopterus luscus* and the black seabream *Spondyllosoma cantharus*, respectively in 13% and 6% of the videos; one at genus level: the dragonet *Callionymus* sp. (26% of the videos); three at the family level: Gobiidae for gobies, Labridae for wrasses and Sparidae for porgies, respectively in 19%, 6% and 6% of the videos; and finally indeterminate

teleost fish (6% of the videos). The common starfish (*Asterias rubens*) was present in one video sequence (3%).

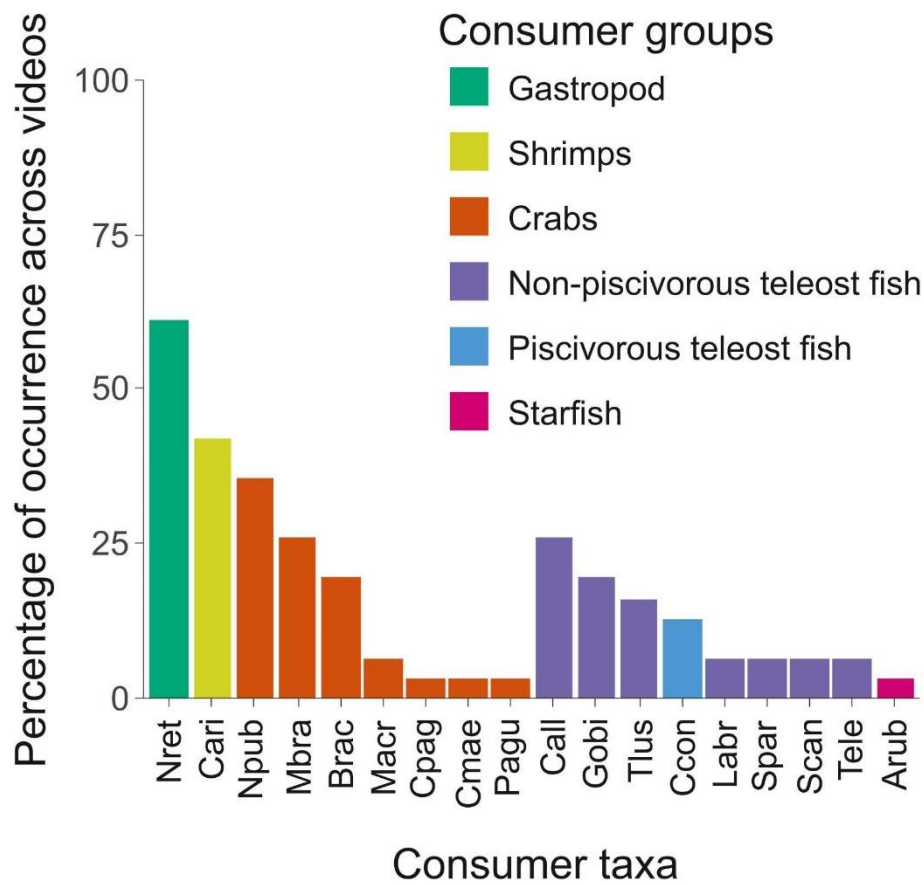


Figure 1. Percentage of occurrence of consumer taxa across videos (n=31). Colors represent consumer groups (according to their different morphological, locomotion and trophic traits). Nret = *Nassarius reticulatus*, Cari = Caridea, Npub = *Necora puber*, Mbra = *Maja brachydactyla*, Macr = *Macropodia* sp., Cpag = *Cancer pagurus*, Cmae = *Carcinus maenas*, Pagu = *Pagurus* sp., Call = *Callionymus* sp., Gobi = Gobiidae, Tlus = *Trisopterus luscus*, Ccon = *Conger conger*, Labr = Labridae, Scan = *Spondyliosoma cantharus*, Spar = Sparidae, Acti = Actinopterygii, Arub = *Asterias rubens*.

Taxonomic richness (mean $\pm$ SD) was 3 ± 1.5 across all videos, with a minimum of one and a maximum of seven co-occurring taxa observed at the scale of the video. Multiple linear

regression revealed no significant effect of any of the environmental or experimental variables tested on discard consumers taxonomic richness across videos (Delta AICc < 2 averaged model), except a significant positive effect of video length ($z = 2841$, $p\text{-value} = 0.005$) (Table A.1, Figure A.3 and A.4).

3.2 Consumers detection time, chronology of arrival and co-occurrence patterns

All video sequences were analyzed together since they were conducted in a reduced area where environmental variation (e.g. sediment granulometry, vegetation) occurs in a patchy distribution at a very low spatial scale and there was no significant effect of any of those environmental variables on taxonomic richness of discard consumers. In addition, all observed taxa are mobile opportunistic feeders without strict microhabitat affiliation. Consumers depicted significantly different times of arrival to the discard according to their group (PERMANOVA: Pseudo- $F_{5-93} = 4.11$, $p\text{-value} = 0.003$; starfish were not included as there was only one observation) (Figure 2). *N. reticulatus* was the quickest to arrive on discards according to post hoc pairwise tests ($t_{43} = 2.39$, $p = 0.021$, $t_{30} = 3.17$, $p = 0.004$, $t_{47} = 2.82$, $p = 0.007$ and $t_{22} = 6.45$, $p < 0.001$ against non-piscivorous teleost fish, shrimps, crabs and piscivorous teleost fish, respectively) (Table A.2), with a median (minimum-maximum) time of arrival of the first individual of 6 min (0-78). Non-piscivorous teleost fish, shrimps and crabs were overlapping in their arrival time (non-significant *post hoc* pairwise tests), being 18 min (1-313), 23 (1-114) and 37 min (0-314), respectively. The only starfish *Asterias rubens* arrived after 28 min on the discard, falling within the same window of first arrival time as crabs, shrimps and non-piscivorous teleost fish. The only piscivorous teleost fish *Conger conger* arrived significantly later than all other groups ($t_{16} = 3.37$, $p = 0.004$, $t_{33} = 2.35$, $p = 0.023$ and $t_{29} = 2.70$, $p = 0.013$

against shrimp, crabs and non-piscivorous teleost fish, respectively), with a median time of arrival of 132 min (45-242).

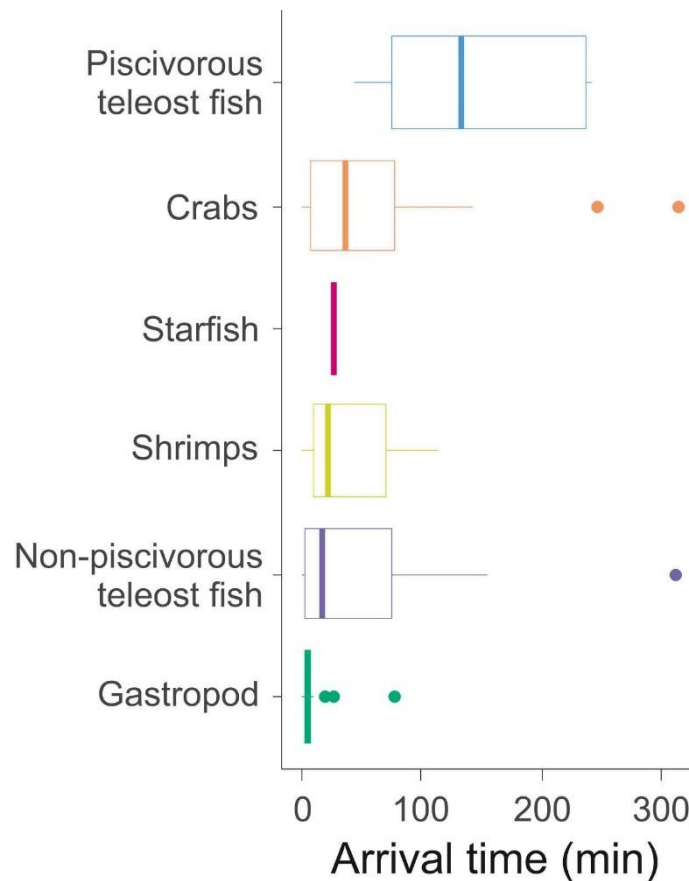


Figure 2. Time of arrival of the first individual of each taxon (in minutes) on the discard across videos (n=31). Taxa are grouped according to their different morphological, locomotion and trophic traits (light blue = piscivorous teleost fish, orange = crabs, pink = starfish, yellow = shrimps, purple = non-piscivorous teleost fish and green = gastropod).

In terms of chronology of arrival to the discards across all video sequences, *N. reticulatus* most frequently arrived first. It was present in 61% of the videos, arriving first in 48%, second in 10% and fourth in the remaining 3% (Figure 3). Crabs dominated the second position in the chronology, arriving second in 39% of the videos, including *N. puber* (10%), *M.*

brachydactyla (13%), *Macropodia* sp. (3%), *C. pagurus* (3%) and indeterminate Brachyura (10%). Non-piscivorous teleost fish dominated the third position (i.e. 29% of the videos), and were more diversified in terms of taxonomic richness after the peak of decapods arrival in second position. Non-piscivorous teleost fish arriving in third position included *T. luscus* (3%), *S. cantharus* (7%), Sparidae (3%), Gobiidae (7%), *Callionymus* sp. (7%) and indeterminate teleost fish (3%). Crabs and teleost fish (including both non-piscivorous and piscivorous species) remained the dominant groups to arrive on the discards from the fourth to the seventh position in the chronology of arrival.

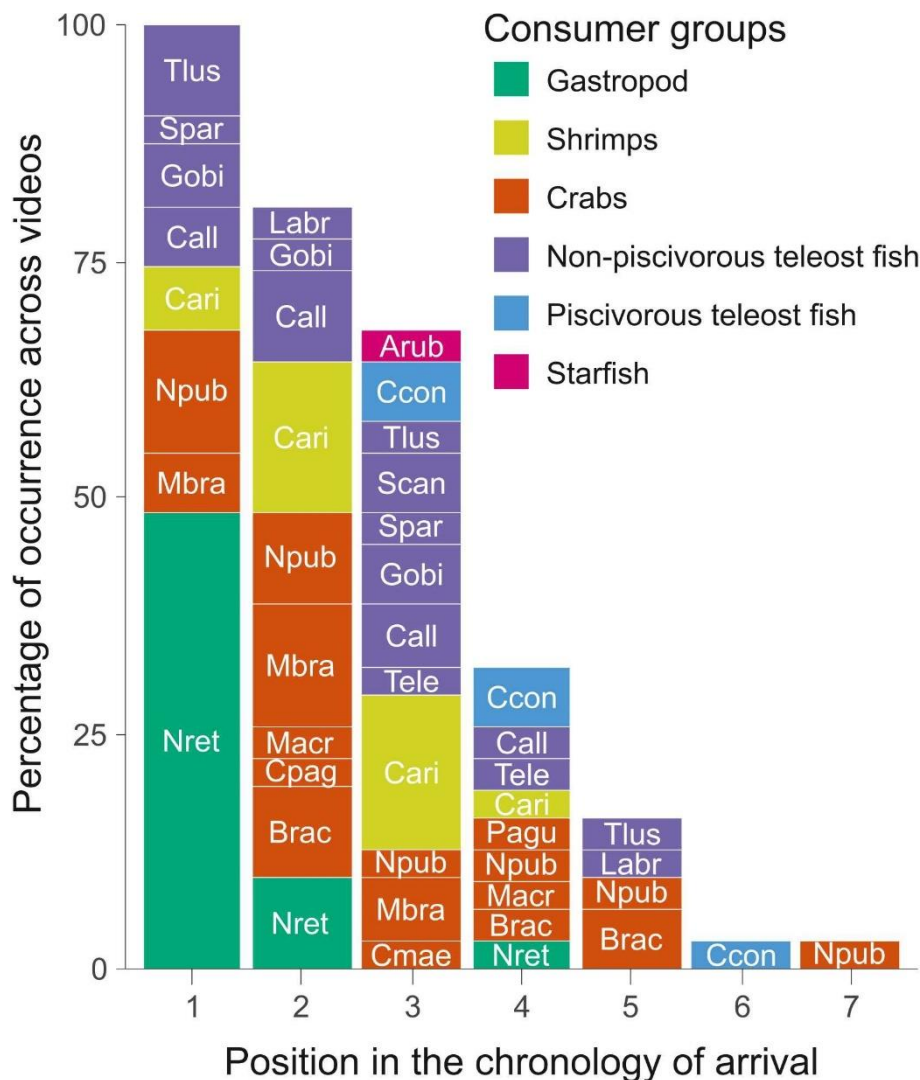


Figure 3. Chronology of arrival of the consumers on discards across videos (n = 31). The position of each taxon in the chronology is based on the time of arrival of the first individual of

each taxon on the discard in each video. Colors represent consumer groups as described in Figure 2. See Fig. 1 caption for acronym details.

There was a total of 36 possible taxa pairs from the presence-absence data matrices, out of which 2 were positive (6%) with taxa co-occurring more frequently than expected, 1 was negative (3%) with taxa co-occurring less frequently than expected, and 33 were random (92%) (Figure 4a and 4b). Significant positive co-occurrences were observed between *N. reticulatus* vs. Caridea (p-value < 0.001) and *M. brachydactyla* vs. *C. conger* (p-value = 0.043) (Figure 4a). Significant negative co-occurrence ($\alpha < 0.05$) was observed between *N. puber* vs. *N. reticulatus* (p-value = 0.042). Negative co-occurrence could be considered marginally significant between *T. luscus* and Caridea (p-value = 0.05) (Table A.3; Table A.4). *C. conger* was the species depicting the highest proportion of positive associations with other species (20% of pairings) while *N. puber* was the species depicting the highest proportion of negative associations with other species (12.5% of pairings) (Figure 4b).

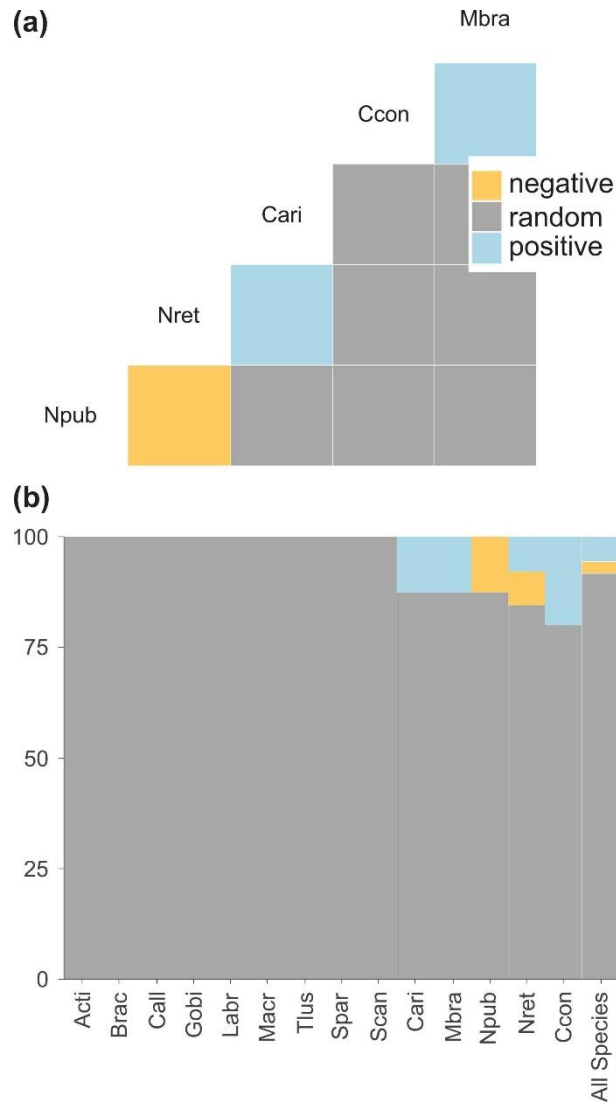


Figure 4. Consumers' co-occurrence analysis. (a) Heatmap of pairwise associations between taxa determined through probabilistic modelling of co-occurrences showing taxa involved in positive and negative interactions at the scale of entire video length. Taxa that co-occur more frequently than expected by chance ($\alpha \leq 0.05$) are considered to have a positive association (blue), those that co-occur less frequently than by chance are considered to have a negative association (yellow), with random associations shown in gray; and (b) Cumulative percentage of total pairings for each taxon that are positive, negative, or random. Taxa are ordered by increasing number of total associations. The right-most bar, outlined in white, represents the assemblage-wide percentages. See Fig. 1 caption for acronym details.

3.3 Analysis of consumer successions and behavioral interactions

19 of the 31 videos contained behavioral interactions. There were 5 succession events, 15 interspecific repulsions, 25 intraspecific repulsions and 1 positive interaction. All 5 succession events (i.e. without displaying antagonistic behaviors) concerned non-piscivorous teleost fish (*T. luscus*, *S. cantharus*, Gobiidae and indeterminate teleost fish) coming to consume discards right after the departure of crabs (*M. brachydactyla*, *N. puber* and *Pagurus* sp.) (Figure A.5). The 15 interspecific repulsions involved 7 different taxa: *C. pagurus*, *C. conger*, *A. rubens*, *M. brachydactyla*, *N. puber*, *N. reticulatus* and Caridea (Figure 5; Figure A.6). *N. reticulatus* was the most repelled taxon (11 out of 15 interspecific repulsions events). They were observed to be repelled by: *M. brachydactyla* (36.4% of repulsion events directed towards *N. reticulatus*), *N. puber* and *C. conger* (both 27.3% of repulsion events) and *A. rubens* (9.1% of repulsion events). Whenever possible, analysis of the variation of *N. reticulatus* abundance in relation to the presence of repulsive species revealed an important decrease prior to the arrival of the decapods *M. brachydactyla* and *N. puber* and subsequent increase following their departure from the discards (Figure A.7). *N. reticulatus* abundance also decreased following the arrival of the starfish *A. rubens*. Caridea were repelled by *N. puber* in 100% of cases. *M. brachydactyla* was repelled in 50% of cases by *C. conger* and 50% by *C. pagurus*. Repulsion events (hunting, escaping or pushing each other) were observed between individuals of the same species in: *N. reticulatus* (n = 2); *T. luscus* (n = 13); *Callionymus* sp. (n = 1); *N. puber* (n = 1) and Brachyura (n = 8). One potential positive interaction was observed between *T. luscus* and *N. puber*, the first being observed to consume pieces of the discard scattered around the BRUVs by feeding *N. puber*.

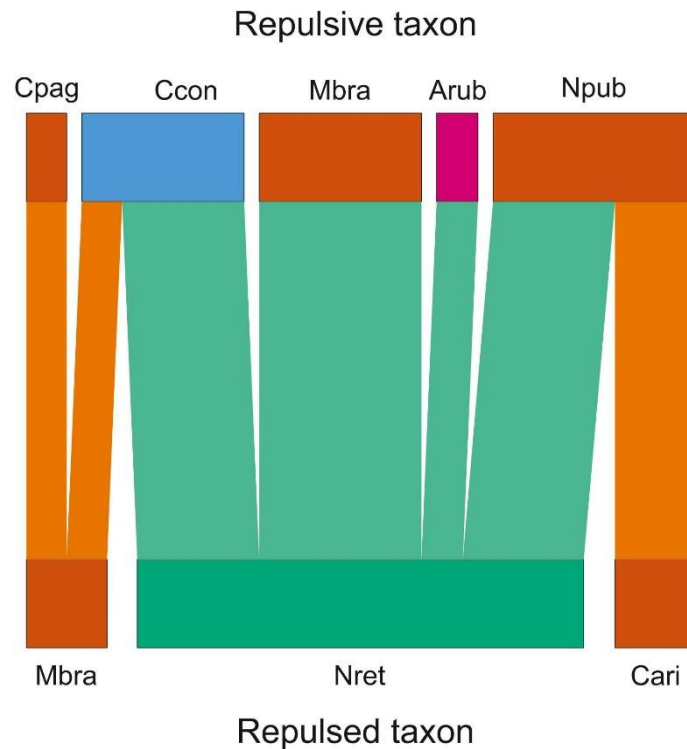


Figure 5. Bipartite network of the observed interspecific antagonistic behaviors (i.e. repulsion events) between repulsive taxa (top) and repulsed taxa (bottom). Rectangles representing taxa are colored according to the consumer groups described in Figure 2 and links between taxa are colored according to the consumer group of the repulsed taxon. Rectangle length and link width are proportional to the number of repulsive events involved. See Figure 1 caption for acronym details.

4. Discussion

4.1 Diversity of discard consumers

Based on baited remote underwater video analysis, we identified 18 discard consumer taxa belonging to piscivorous and non-piscivorous teleost fish, crabs (including hermit crabs and spider crabs), shrimps, one gastropod and one starfish in shallow fishing grounds of the bay of Bourgneuf. The main discard consumers were netted dog whelks (gastropod), Caridea shrimps,

velvet crabs, common spider crabs and dragonets (non-piscivorous teleost fish). Among all taxa observed to consume discards, only the netted dog whelk (*N. reticulatus*) is considered an obligate scavenger (Ruxton and Houston, 2004) and only the European conger (*C. conger*) belongs to the piscivore trophic guild (Thompson et al., 2020). This suggests that in fishing grounds, facultative scavenging behaviors towards discarded fish may be relatively common among non-typically scavenging and non-piscivorous marine consumers. Most observed consumers are generalist and opportunistic taxa with a flexible feeding ecology, but whose piscivory or dietary dependence on carrion is considered to be low or never precisely assessed. For example, the velvet crab *N. puber* is an omnivore that feeds mainly on benthic invertebrates or brown algae depending on its ontogenetic stage, and only occasionally on fish likely consumed as carrion (Freire and González-Gurriarán, 1995; MarLIN, 2006; Norman and Jones, 1992). Other decapods identified as discard consumers in this study show similar feeding plasticity, such as *M. brachydactyla*, *C. maenas* and *C. pagurus* (Baeta et al., 2006; Bernárdez et al., 2000; MarLIN, 2006), and generally low trophic levels (Palomares and Pauly, 2021; Pauly et al., 2020). Because spatial variability in the availability of prey has been identified as the primary cause of change in the trophic strategies of decapods (Edgar, 1990; Freire and González-Gurriarán, 1995; González-Gurriarán et al., 1989), they may rely more on discards where discarding practices are more common, as suggested in this study. Gut content metabarcoding analysis of marine fauna in fishing grounds of the Bay of Bourgneuf revealed that discard ingestion may be widespread across benthic-demersal consumers but more important in decapods (Lejeune et al., 2022b). Based on the analysis of muscle isotopic composition, a previous study in the same area also found that decapods depicted a high trophic level which may be explained by substantial reliance on fisheries discards (Lejeune et al., 2022a). But in the stable isotope study, evidence of discard consumption by fish was limited. The authors interpreted this as resulting either from an absence of consumption of discards by

most fish or the opportunistic consumption of other low trophic level prey displaced by trawling, which could counterbalance any visible effect of discard consumption on their isotopic composition. In this study, we can confirm that decapods but also a variety of teleost fish are effectively attracted by and able to consume discards. This echoes with research conducted in different environmental settings showing that demersal fish such as dragonets, gobies, pout (*T. luscus*) and other benthic-pelagic opportunistic predatory fish such as wrasses and porgies opportunistically scavenge upon discards or carrion generated by trawling (e.g. Groenewold and Fonds 2000; Jenkins et al. 2004; Depesstele et al. 2019). Interestingly, the only piscivorous species (*C. conger*) arrived significantly later than all other consumer groups and acted like a discard “finisher”, swallowing the discard whole.

4.2 Utility of underwater videos to elucidate consumption dynamic and species interactions around discards

Analyses of detection time and chronology of arrival of discard consumers revealed that the only obligate scavenger, the gastropod *N. reticulatus*, was the quickest to arrive on carcasses as well as the most occurring taxa (i.e. > 60% of the videos). Although we do not have information on species abundance in the area of study, this may be linked to a higher density of *N. reticulatus*. Yet, *N. reticulatus* is also known to possess a well-developed olfactory system allowing it to rapidly detect and locate carrion in the environment (Davenport and Moore, 2002). Being a potential prey for many other discard consumers, *N. reticulatus* was also the most subject to repulsion by others. As such, *N. reticulatus* individuals could generally be seen leaving the discard whenever other consumers would arrive (except shrimps and gobies). In several videos, *N. reticulatus* could even be seen massively leaving the discard < 10 min prior to the arrival of *N. Puber* and *M. brachydactyla* within the frame of the camera. These mass movements might correspond to the detection of potential predator arrivals, i.e. antipredator

behaviors. Indeed, previous experimental work revealed that thanks to their well-developed olfactory system, starved *N. reticulatus* remain hidden whenever they detect damaged conspecifics likely as an antipredator response (Davenport and Moore, 2002). Yet in our case, this remains speculative and further studies are needed to clearly test the ability of *N. reticulatus* to detect predators to some distance and initiate an escape. The observed behavioral interactions might also explain the negative association between *N. reticulatus* and *N. puber*, or the marginally significant one between *N. reticulatus* and *T. luscus* in co-occurrence analysis, as they are known predators of gastropods (Froese and Pauly, 2021; Palomares and Pauly, 2021; Thompson et al., 2020).

Crabs and non-piscivorous teleost fish were most occurrent in the second and third position of the chronology of arrival, respectively. Direct observations of interactions between consumers revealed that the departure of decapods such as *N. puber* and *M. brachydactyla* was followed by a quick arrival of fish in several videos, which is consistent with the fact that fish tend to avoid approaching carrion whenever crabs are already at it (Davenport et al., 2016). Yet interestingly, *T. luscus* could also be seen taking advantage of the wasteful feeding of crabs by consuming pieces of discards being scattered around by *N. puber*, allowing them to consume discards at the same time as crabs while avoiding potential aggressive behaviors by staying at a distance. This suggests that crabs might more generally facilitate the consumption of discards by non-typically scavenger or non-piscivorous fish, despite the fact that they are potential competitors. All teleost fish attracted by discards in this study are non-piscivorous species (Thompson et al., 2020) and may be considered ill-equipped to consume discarded fish (i.e. small gape size or low bite force), except *C. conger*. They may therefore benefit from the presence of other species to dismantle it first. Davenport et al. (2016) also showed that crabs are generating scraps for indirect feeders when scavenging on carrion, resulting in the attraction of more scavengers. In a study using scallop baits, Jenkins et al. (2004) also noted that the

scavenger community was relying on crabs breaking open the scallop shells to consume them, with fish seen waiting and feeding at the chelae of crabs on many occasions. Likewise, extra-oral digestion of fish skin by *Asterias rubens* can facilitate scavenger feeding on fish prey (Ramsay et al., 1997).

Direct observations of interactions between consumers also revealed many intraspecific repulsion events suggesting interference competition between conspecifics, especially in crabs. Threat displays are well known in crabs which can ‘elbow’ with the carpus of the cheliped both for aggression and to space each other around carcasses (Davenport et al., 2016). Moreover, we noted that threat displays between crabs generated a lot of sediment dispersion, which might dissuade other species from getting close. Positive associations between *C. conger* and *M. brachydactyla* or *N. reticulatus* and *Caridea* revealed by co-occurrence analysis could suggest that the species involved are attracted by the same type of discard or that they have similar microhabitat preferences. These results, together with observations from the literature (e.g. Jenkins et al. 2004), illustrate how video analysis can provide valuable information to verify or understand the ability of a species to consume discards and better understand the dynamic of discard consumption by marine fauna. The fact that taxonomic richness increased with video length suggests that longer videos could further increase the richness of observed taxa and the occurrence of behavioral interactions, as well as identify other species which could potentially only consume discards in a state of advanced degradation. However, this also increases the probability of large piscivores, such as *C. conger* to find the discard and consume it whole, as observed in this study. Finally, one may expect that different discarded species would attract different scavengers or affect detection time due to differences in nutritional composition (e.g. mackerel being a fatty fish is likely very different from the other discarded species used in this study). Low sample size did not allow us to test such an effect here, but future studies aiming to characterize attraction towards different types of discards depending on their nutritional

composition may allow to predict which species would likely be attracted based on the composition of discarded fish community in a given area or season.

4.3 Understanding the impact of fisheries discards and their reduction on marine food webs

Fisheries discard rates (i.e. animals caught, but returned to the sea, dead or alive, as a result of low commercial value, under quota restriction, below the minimum allowable size or damaged) are estimated to represent ~10 % of global annual catches (Zeller et al., 2018), but may vary considerably at lower spatial scale. Discarding practices have recently been recognized as a source of concern for the perennation of marine resources, prompting global efforts towards their reduction (Zeller et al., 2018). However, effects of such measures on populations, communities and ecosystem functioning, whether beneficial or detrimental, direct or indirect, are still unclear (e.g. Kopp et al., 2016; Sherley et al., 2019). A better understanding of facultative scavenging and its importance across marine fauna is key to forecast the impact of discarding practices on food web structure and functioning in fishing grounds, as well as anticipate potential food web changes linked to the implementation of discard bans in many areas around the globe (Depestele et al., 2019). This study constitutes a first step towards a better understanding of facultative scavenging abilities across benthic fauna in the shallow fishing grounds of the Bay of Bourgneuf. Together with previous indications of discard ingestion and assimilation in the same fishing ground obtained via stable isotopes (Lejeune et al., 2022a) and DNA metabarcoding of gut contents (Lejeune et al., 2022b), our study suggest that many low trophic level benthic taxa (e.g. decapods, small fish, mollusks) may be important nodes to consider for the reintegration of discards within the marine food web. Because these are potentially important prey at the base of the food web and some (e.g. decapods) are known

to play structuring roles within benthic communities, reducing discards might propagate changes across the food web via these important species (Lejeune et al., 2022b).

5. Conclusions

The use of underwater videos offers unique insights in terms of characterization of consumption dynamic and species associations or interactions around discards which ultimately allow to understand and objectify the existence of trophic links between consumers and discards. Better knowledge on trophic links with discards constitutes one of the challenges of understanding fisheries discards reintegration into marine food webs (Depestele et al., 2019; Guillen et al., 2018). Ecosystem models aiming to depict marine food web and the influence of anthropogenic factors such as fishing or climate change on its dynamic (e.g. Atlantis or Ecopath with Ecosim; Fulton 2010; Heymans et al. 2016) provide contrasting predictions regarding the importance of discards for marine fauna (e.g. Catchpole and Frid 2006; Depestele et al. 2019), partly owing to the lack of empirical studies, especially at local scales. Altogether, we can conclude that in shallow coastal fishing grounds, discards could be consumed by a large diversity of species, both in terms of taxonomic and trophic groups, including low trophic level benthic fish and omnivorous invertebrate macrofauna such as decapods (Froese and Pauly, 2021; Palomares and Pauly, 2021; Thompson et al., 2020). This supports previous research suggesting that the diversity of discard consumers may currently be underestimated (Guillen et al., 2018; Lejeune et al., 2022b, 2022a). Whether such behaviors correspond to stable trophic strategies over time remains to be established, notably through repeated measures and an integrated use of multiple diet assessment techniques (e.g. gut content, stable isotopes, fatty acids or other trophic tracers) (Lejeune et al., 2021).

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6. References

- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: A guide to software and statistical methods. PRIMER-E, Plymouth, UK.
- Baeta, A., Cabral, H.N., Margues, J.C., Pardal, M.A., 2006. Feeding ecology of the green crab, *Carcinus maenas* (L., 1758) in a temperate estuary, Portugal. *Crustaceana* 79, 1181–1193.
- Bartoń, K., 2016. MuMIn: Multi-model inference [WWW Document]. URL <https://cran.r-project.org/package=MuMIn>
- Beasley, J.C., Olson, Z.H., DeVault, T.L., 2015. Ecological role of vertebrate scavengers, in: Benbow, E.M., Tomberlin, J., Tarone, A. (Eds.), *Carrion Ecology, Evolution, and Their Applications*. CRC Press, Boca Raton, Florida, USA, pp. 107–127.
<https://doi.org/10.1201/b18819-8>
- Bernárdez, C., Freire, J., González-Gurriarán, E., 2000. Feeding of the spider crab *Maja squinado* in rocky subtidal areas of the Ría de Arousa (north-west Spain). *J. Mar. Biol. Assoc. United Kingdom* 80, 95–102. <https://doi.org/10.1017/S0025315499001605>
- Catchpole, T., Frid, C.L.J., 2006. Importance of discards from the English *Nephrops norvegicus* fishery in the North Sea to marine scavengers. *Mar. Ecol. Prog. Ser.* 313, 215–226. <https://doi.org/10.3354/meps313215>

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

Cornou, A., Quinio-scavinner, M., Sagan, J., Cloâtre, T., Dubroca, L., Billet, N., 2021.

Captures et rejets des métiers de pêche français. Résultats des observations à bord des navires de pêche professionnelle en 2019. Obsmer.

<https://doi.org/https://doi.org/10.13155/79198>

Davenport, J., McCullough, S., Thomas, R.W., Harman, L., Mcallen, R., 2016. Behavioural responses of shallow-water benthic marine scavengers to fish carrion: a preliminary study. *Mar. Freshw. Behav. Physiol.* 49, 301–315.

<https://doi.org/10.1080/10236244.2016.1205793>

Davenport, J., Moore, P.G., 2002. Behavioural responses of the netted dogwhelk *Nassarius reticulatus* to olfactory signals derived from conspecific and nonconspecific carrion. *J. Mar. Biol. Assoc. United Kingdom* 82, 967–969.

<https://doi.org/10.1017/S002531540200646X>

Depestele, J., Feekings, J., Reid, D.G., Cook, R., Gascuel, D., Girardin, R., Heath, M.,

Hervann, P.-Y., Morato, T., Soszynski, A., Savina-Rolland, M., 2019. The Impact of Fisheries Discards on Scavengers in the Sea, in: Uhlmann, S.S., Ulrich, C., Kennelly, S.J. (Eds.), *The European Landing Obligation: Reducing Discards in Complex, Multi-Species and Multi-Jurisdictional Fisheries*. Springer International Publishing, Cham, pp. 129–162. https://doi.org/10.1007/978-3-030-03308-8_7

Depestele, J., Rochet, M., Dorémus, G., Laffargue, P., Stienen, E.W.M., 2016. Favorites and leftovers on the menu of scavenging seabirds: modelling spatio-temporal variation in discard consumption. *Can. J. Fish. Aquat. Sci.* 73, 1446–1459.

<https://doi.org/10.1139/cjfas-2015-0326>

- Dormann, C.F., Frund, J., Gruber, B., 2008. Introducing the bipartite package: Analysing ecological networks. *R News* 8, 8–11.
- Edgar, G.J., 1990. Predator-prey interactions in seagrass beds. II. Distribution and diet of the blue manna crab *Portunus pelagicus* Linnaeus at Cliff Head, Western Australia. *J. Exp. Mar. Bio. Ecol.* 139, 23–32.
- Freire, J., González-Gurriarán, E., 1995. Feeding ecology of the velvet swimming crab *Necora puber* in mussel raft areas of the Ría de Arousa (Galicia, NW Spain). *Mar. Ecol. Prog. Ser.* 119, 139–154.
- Froese, R., Pauly, D., 2021. FishBase [WWW Document]. URL www.fishbase.org (accessed 2.6.21).
- Fulton, E.A., 2010. Approaches to end-to-end ecosystem models. *J. Mar. Syst.* 81, 171–183. <https://doi.org/10.1016/j.jmarsys.2009.12.012>
- Garthe, S., Camphuysen, K.C., Furness, R.W., 1996. Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Mar. Ecol. Prog. Ser.* 136, 1–11. <https://doi.org/10.3354/meps136001>
- Gauduchon, T., Cornou, A., Quinio-Scavinner, M., Goascoz, N., Dubroca, L., Billet, N., 2020. Captures et rejets des métiers de pêche français. Résultats des observations à bord des navires de pêche professionnelle en 2018. *Obsmer*. <https://doi.org/10.13155/73122>
- González-Gurriarán, E., Freire, J., Fernández, L., Poza, E., 1989. Incidencia del cultivo de mejillón en la dieta de *Liocarcinus depurator* (L.) (Brachyura: Portunidae) en la Ría de Arousa (Galicia, NW España). *Cah. Biol. Mar.* 30, 307–319. <https://doi.org/10.21411/CBM.A.A949F22A>
- Griffith, D.M., Veech, J.A., Marsh, C.J., 2016. cooccur: Probabilistic species co-occurrence

- analysis in R. *J. Stat. Softw.* 69, 1–17. <https://doi.org/10.18637/jss.v069.c02>
- Groenewold, S., Fonds, M., 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. *ICES J. Mar. Sci.* 57, 1395–1406. <https://doi.org/10.1006/jmsc.2000.0914>
- Guillen, J., Holmes, S.J., Carvalho, N., Casey, J., Dörner, H., Gibin, M., Mannini, A., Vasilakopoulos, P., Zanzi, A., 2018. A review of the European union landing obligation focusing on its implications for fisheries and the environment. *Sustainability* 10, 900. <https://doi.org/10.3390/su10040900>
- Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecol. Modell.* 331, 173–184. <https://doi.org/10.1016/j.ecolmodel.2015.12.007>
- Jenkins, S.R., Mullen, C., Brand, A.R., 2004. Predator and scavenger aggregation to discarded by-catch from dredge fisheries : importance of damage level. *J. Sea Res.* 51, 69–76. <https://doi.org/10.1016/j.seares.2003.05.002>
- Kopp, D., Robert, M., Chouvelon, T., Méhault, S., 2016. Some expected impacts of the Common Fishery Policy on marine food webs. *Mar. Policy* 66, 8–14. <https://doi.org/10.1016/j.marpol.2016.01.002>
- Laptikhovsky, V., Pompert, J., Brickle, P., 2006. Fishery discard management and environmental impact in Falkland Islands Fisheries, in: Paper Submitted to ICES Conference.
- Lejeune, B., Bissey, L., Didaskalou, E.A., Sturaro, N., Lepoint, G., Denoël, M., 2021. Progenesis as an intrinsic factor of ecological opportunity in a polyphenic amphibian.

- Funct. Ecol. 35, 546–560. <https://doi.org/10.1111/1365-2435.13708>
- Lejeune, B., Kopp, D., Mehault, S., Mouchet, M.A., 2022a. Assessing the diet and trophic level of marine fauna in a fishing ground subject to discarding activity using stable isotopes. PLoS One 6, e0268758. <https://doi.org/10.1371/journal.pone.0268758>
- Lejeune, B., Mouchet, M.A., Mehault, S., Kopp, D., 2022b. Gut content metabarcoding reveals potential importance of fisheries discards consumption in marine fauna. Can. J. Fish. Aquat. Sci. 79, 1064–1073. <https://doi.org/10.1139/cjfas-2021-0267>
- MarLIN, 2006. BIOTIC - Biological Traits Information Catalogue [WWW Document]. Mar. Life Inf. Network. Plymouth Mar. Biol. Assoc. United Kingdom. URL www.marlin.ac.uk/biotic (accessed 2.4.21).
- Martin, J., 2011. Les invertébrés marins du golfe de Gascogne à la Manche orientale. Quae, Versailles, France.
- Morfin, M., Simon, J., Morandeau, F., Baulier, L., Méhault, S., Kopp, D., 2019. Using acoustic telemetry to estimate post-release survival of undulate ray *Raja undulata* (Rajidae) in northeast Atlantic. Ocean Coast. Manag. 178, 104848. <https://doi.org/10.1016/j.ocecoaman.2019.104848>
- Norman, C.P., Jones, M.B., 1992. Influence of depth, season and moult stage on the diet of the velvet swimming crab *Necora puber* (Brachyura , Portunidae). Estuar. Coast. Shelf Sci. 34, 71–83.
- Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514. <https://doi.org/10.1111/ele.12187>
- Palomares, M.L.D., Pauly, D., 2021. SeaLifeBase [WWW Document]. URL

- www.sealifebase.org (accessed 2.6.21).
- Pauly, D., Zeller, D., Palomares, M.-L., 2020. Sea Around Us Concepts, Design and Data (www.seaaroundus.org).
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramsay, K., Kaiser, M.J., Moore, P.G., Hughes, R.N., 1997. Consumption of fisheries discards by benthic scavengers: utilization of energy subsidies in different marine habitats. *J. Anim. Ecol.* 66, 884–896. <https://doi.org/10.2307/6004>
- Ruxton, G.D., Houston, D.C., 2004. Energetic feasibility of an obligate marine scavenger. *Mar. Ecol. Prog. Ser.* 266, 59–63. <https://doi.org/10.3354/meps266059>
- Sherley, R.B., Ladd-Jones, H., Garthe, S., Stevenson, O., Votier, S.C., 2019. Scavenger communities and fisheries waste : North Sea discards support 3 million seabirds, 2 million fewer than in 1990. *Fish Fish.* 21, 132–145. <https://doi.org/10.1111/faf.12422>
- Thompson, M.S.A., Pontalier, H., Spence, M.A., Pinnegar, J.K., Greenstreet, S., Moriarty, M., H  laou  t, P., Lynam, C.P., 2020. A feeding guild indicator to assess environmental change impacts on marine ecosystem structure and functioning. *J. Appl. Ecol.* 57, 1769–1781. <https://doi.org/10.1111/1365-2664.13662>
- Veech, J.A., 2013. A probabilistic model for analysing species co-occurrence. *Glob. Ecol. Biogeogr.* 22, 252–260. <https://doi.org/10.1111/j.1466-8238.2012.00789.x>
- Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E., Caldow, R.W.G., Catry, P., Ensor, K., Hamer, K.C., Hudson, A. V, Kalmbach, E., Klomp, N.I., Pfeiffer, S., Phillips, R.A., Prieto, I., Thompson, D.R., 2004. Changes in fisheries discard rates and seabird communities. *Nature* 427, 727–730. <https://doi.org/10.1038/nature02251.1>.

Zeller, D., Cashion, T., Palomares, M.-L., Pauly, D., 2018. Global marine fisheries discards :
A synthesis of reconstructed data. *Fish Fish.* 19, 30–39. <https://doi.org/10.1111/faf.12233>

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Table A.3: Discard consumers' co-occurrence analysis.

Table A.4: Consumer taxa occurrences in each of the 31 video sequences.

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Figure A.2: Camera footages of some of the different discard consumers.

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Figure A.4: Relation between video length (in minutes) and taxonomic richness of consumers.

Figure A.5: Co-occurrence of consumer taxa across time revealing five succession events in four videos.

Figure A.6: Co-occurrence of consumer taxa across time revealing interspecific repulsions in five videos.

Figure A.7: Variations of *N. reticulatus* abundance in the presence of repulsive taxa in video sequences where *N. reticulatus* abundance was judged sufficient to observe significant variation.