

Preliminary analysis of the feeding habits of two species of the genera *Mobula*, *Mobula japonica* (Müller & Henle, 1841) and *Mobula tarapacana* (Philippi, 1892) in the coastal waters of Côte d'Ivoire, Gulf of Guinea

ABSTRACT

Mobulids are filter feeders, particularly vulnerable to overexploitation due to their late sexual maturation and low fertility. However, knowledge of their biology remains limited, requiring sub-regional and international cooperation to ensure their preservation. This study provides baseline information on the feeding habits of *Mobula japonica* and *Mobula tarapacana* using data on stomach contents. Specimens were sampled from the small-scale driftnet fishery operating along the coast of Côte d'Ivoire between March 2020 and April 2022. Diet was described using the Prey-Specific Index of Relative Importance (%PSIRI) combining occurrence, numerical and weight percentages. A total of 215 *M. tarapacana* and 210 *M. japonica* ranging in sizes of 154–371 cm DW and 80–369 cm DW were examined, respectively. The large number of empty stomachs for *M. japonica* (71.43%) and *M. tarapacana* (73.02%) may be the result of using hooks, which cause high stress resulting in stomach regurgitation. *Mobula japonica* and *M. tarapacana* consumed mainly commonly abundant crustaceans such as *Sergestes atlanticus* and euphausiid *Pseudeuphausia latifrons*, accounting for 95% and 71.13% of the diet, respectively. However, diet of *M. tarapacana* was more diverse, including crabs, algae of the genus *Sargassum*, teleost fishes,

molluscs and insects. Analysis of Costello diagram showed that both species are specialist predators, although *M. japonica* has a more restricted niche. The Morisita-Horn similarity showed no significant changes in diet according fish sizes and marine seasons.

Keywords: Devil rays, diet, *Mobula japonica*, *Mobula tarapacana*, specialist predator, stomach contents, West Africa, Côte d'Ivoire

1. INTRODUCTION

Rays of Mobulid family are pelagic fishes found in shallow and deep waters in tropical, subtropical and temperate coastal waters [1,2,3]. These species have a crucial ecological role, contributing to the regulation of prey populations and the balance of marine ecosystems [4]. In Côte d'Ivoire, they are a common by-catch in artisanal tuna driftnet fishery targeting tunas [5]. The international market demand causes increased fishing pressure, as ray body parts have high economic value for meat, skin and gill plates [6]. Due to their biological characteristics (low natural mortality, slow growth, late sexual maturation and low offspring [7-2], their excessive exploitation could have a serious impact on the renewal of their population. At this time, the entire *Mobula* spp. has been registered in the Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) whereas *M. tarapacana* and *M. japonica* are classified as Vulnerable or Endangered according to the International Union of Conservation of Nature [8-9].

Understanding the diet of fishes is essential in explaining variations in growth, aspects of reproduction, migration and feeding behaviour [10]. According to Costello [11], it provides information on the diversity of prey ingested, food preferences and trophic niche. For Stewart et al. [12], analysing feeding habits of tropical populations will determine diet preference and allow inference on habitat use and feeding behaviour, which are both very important to the conservation and management of rays. Although studies on the biology and ecology of Mobulid species started since the 17th century, information on their feeding habits still very limited [12]. Couturier et al. [1] reported that their diet is based on zooplankton and ichthyoplankton, but specific differences can occur. For instance, *M. thurstoni* is known to feed on mysid shrimps and euphausiids [13] whereas *M. mobular*, *M. hypostoma*, *M. rochebrunei*, *M. tarapacana*, *M. birostris*, *M. alfredi*, *M. japonica*, and *M. munkiana* feed generally on small fishes and crustaceans like krill (*Meganyctiphanes norvegica*, *Nyctiphanes simplex*), the mysid *Mysidium* sp., and other planktonic organisms [13, 14, 1]. However, no information is known on the feeding habits of *M. tarapacana* and *M. japonica* in the central eastern Atlantic and specifically in the Gulf of Guinea. Thus, the aim of this work is to analyse the composition of their stomach contents and deduce their feeding habits.

2. MATERIALS AND METHODS

Study area

This study was carried out in the Exclusive Economic Zone (EEZ) of Côte d'Ivoire, bordering the Gulf of Guinea (Atlantic Ocean). This zone extends from Cape des Palmes (8°W) in the West to Cape Three Points (2°30'W) in the East [15], over a length of about 600 km (Fig. 1). Its characteristic is the presence of four marine seasons including two warm seasons (March–June and November–December) and two cold seasons (July–October and January–February) [16]. The surface sea water temperatures vary from 27.0 to 30.6°C and the salinity below 35‰.

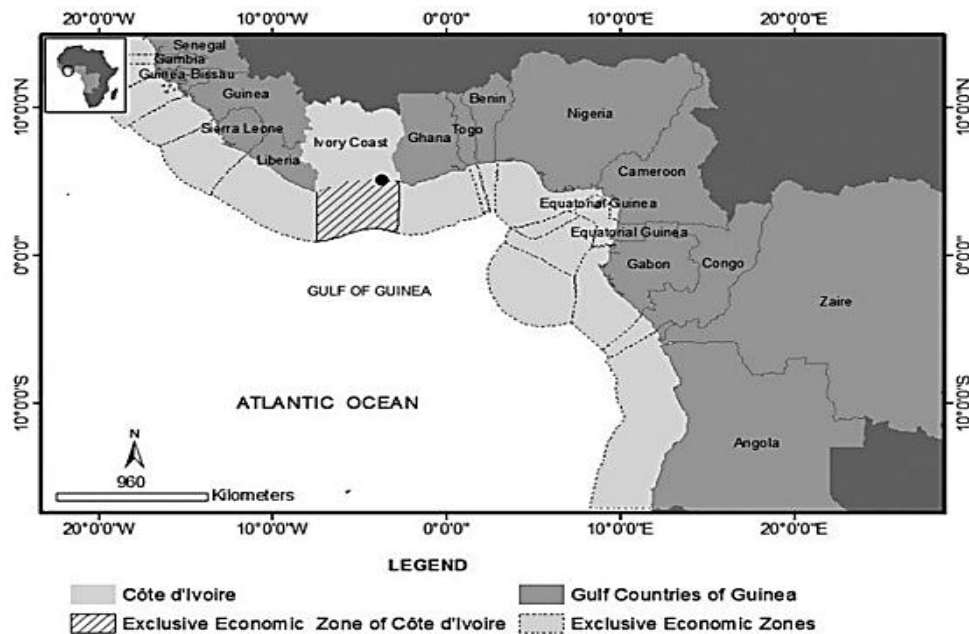


Fig. 1. Map showing the Exclusive Economic Zone (EEZ) of Côte d'Ivoire and the study site.

Sampling and laboratory analysis

Samples were obtained monthly at the fishing harbour of Abidjan (Côte d'Ivoire) from March 2020 to April 2022. For each individual, the sex was determined and the body weight was recorded to the nearest kg. The disc width (DW) was then measured to the nearest 0.1cm using a measuring tape. After dissection, stomachs were removed and kept frozen at –20°C for further analysis in the biology laboratory of the Oceanological Research Centre, Abidjan.

In the laboratory, the stomach contents were washed individually under running water using a 0.5 mm mesh sieve, which retained any undigested food elements in the faeces that could be used for identification (e.g. scales, otoliths, exoskeletons, teeth, etc.). Each prey was then identified to the lowest taxonomic level according to the identification keys of Fisher et al. [17], Schneider [18] and Carpenter et al. [19] and weighed in grams (g). The preys were then counted and weighted and all undetermined preys were considered as unknown preys and classified into a group.



Fig. 2. Species of *Mobula* landed at the fishing harbour of Abidjan (Côte d'Ivoire) from March 2020 to April 2022. **a =** *Mobula tarapacana*, **b =** *Mobula japonica*.

Data analysis

The index of vacuity was used to express the number of empty stomachs encountered as a percentage of the total stomachs examined.

$$\%CV = \frac{\text{Number of empty stomachs}}{\text{Total number of stomachs}} \times 100$$

The contribution of each prey item to the diet was assessed using the prey-specific relative importance index (%PSIRI), as %FO was found to be unknowingly squared in the IRI calculation [20]. The frequency of occurrence (FO), the average percentage abundance (%A_i) and the prey-specific abundance (%PA_i) were calculated with the following equations:

Prey-specific abundance (%PN_i, %PW_i):

$$\%PA_i = \frac{\sum_{j=1}^n \%A_{ij}}{n_i}$$

Average percentage abundance (%N_i, %W_i):

$$PA_i = \frac{\sum_{j=1}^n \%A_{ij}}{n}$$

Frequency of occurrence (FO):

$$\%FO = \frac{n_i}{n}$$

where %A_{ij} is the abundance (by counts or weights) of prey category i in stomach sample j, n_i is the number of stomachs containing prey i, and n is the total number of stomachs.

The %PSIRI was then calculated:

$$\%PSIRI_i = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2}$$

where %FO_i is the percent frequency of occurrence (the number of stomachs containing prey category i divided by the total number of stomachs n) and %PN_i and %PW_i are the prey-specific abundances by counts and weight, respectively.

The classification of prey items followed the method of Rosecchi and Nouaze [21]. For this purpose, preys were first sorted in decreasing order of importance according to their PSIRI and then a cumulative %PSIRI was calculated. The first single item, or group of items, for which cumulative %PSIRI was ≥ 50% was regarded as the preferred food. The %PSIRI values of other important prey items were then added to that of the preferred food until the %PSIRI reached 75%, and

these were regarded as secondary prey. Food items between a %PSIRI of 75 and 100% were regarded as incidental prey. The food Overlaps between sexes and marine seasons were analysed using the Morisita [22] Index as follow:

$$C\lambda = \frac{2 \sum_{i=1}^n (P_{ix} \times P_{iy})}{(\sum_{i=1}^n P_{ix}^2 + \sum_{i=1}^n P_{iy}^2)}$$

Where $C\lambda$ the Morisita-Horn [22] index, P_{ix} and P_{iy} are proportions (based on %PSIRI) of a prey i consumed by the predator x and y respectively, following the sex and marine seasons. Values between 0 and 0.29 indicate a lower overlap, between 0.30 and 0.59 a medium overlap, and values over 0.60 show a higher overlap [23]. The Spearman's ranks correlation coefficient was also used to test the similarity of diet between all categories.

Food strategy

The Costello diagram [24] modified by Amundsen et al. [25] was used to describe the feeding strategies of the species studied. This diagram illustrates the specific abundance of the prey (S_i) as a function of the frequency of occurrence (%FO) and allows analysis of the importance of the prey, the feeding strategy and the contribution to the niche. The prey-specific abundance was determined through following formula:

$$\%S_i = \left(\sum P_i / \sum P \right) \times 100$$

Where P_i = weight of the prey i and P = total weight of preys into stomach containing prey i .

3. RESULTS AND DISCUSSION

Results

Vacuity index

A total of 215 specimens of *M. tarapacana* and 210 specimens of *M. japonica* with sizes ranging from 154 to 371 cm DW and from 80 to 369 cm DW were used, respectively. Of the stomachs examined, 59 (27.44%) had food and 156 (72.56%) were empty in *M. tarapacana* whereas 60 (28.57%) were full and 150 (71.43%) were empty in *M. japonica*. The vacuity index varied slightly according to marine seasons. For *M. japonica*, the vacuity index was higher in the warm season (78.18%) than in the cold season (69.68%). In contrast, the values were higher in the cold season (79.81%) than in the warm season (65.77%) for *M. tarapacana*. However, differences were not statistically significant ($\chi^2 = 0.489$, $p > 0.05$; $\chi^2 = 1.354$, $p > 0.05$, respectively).

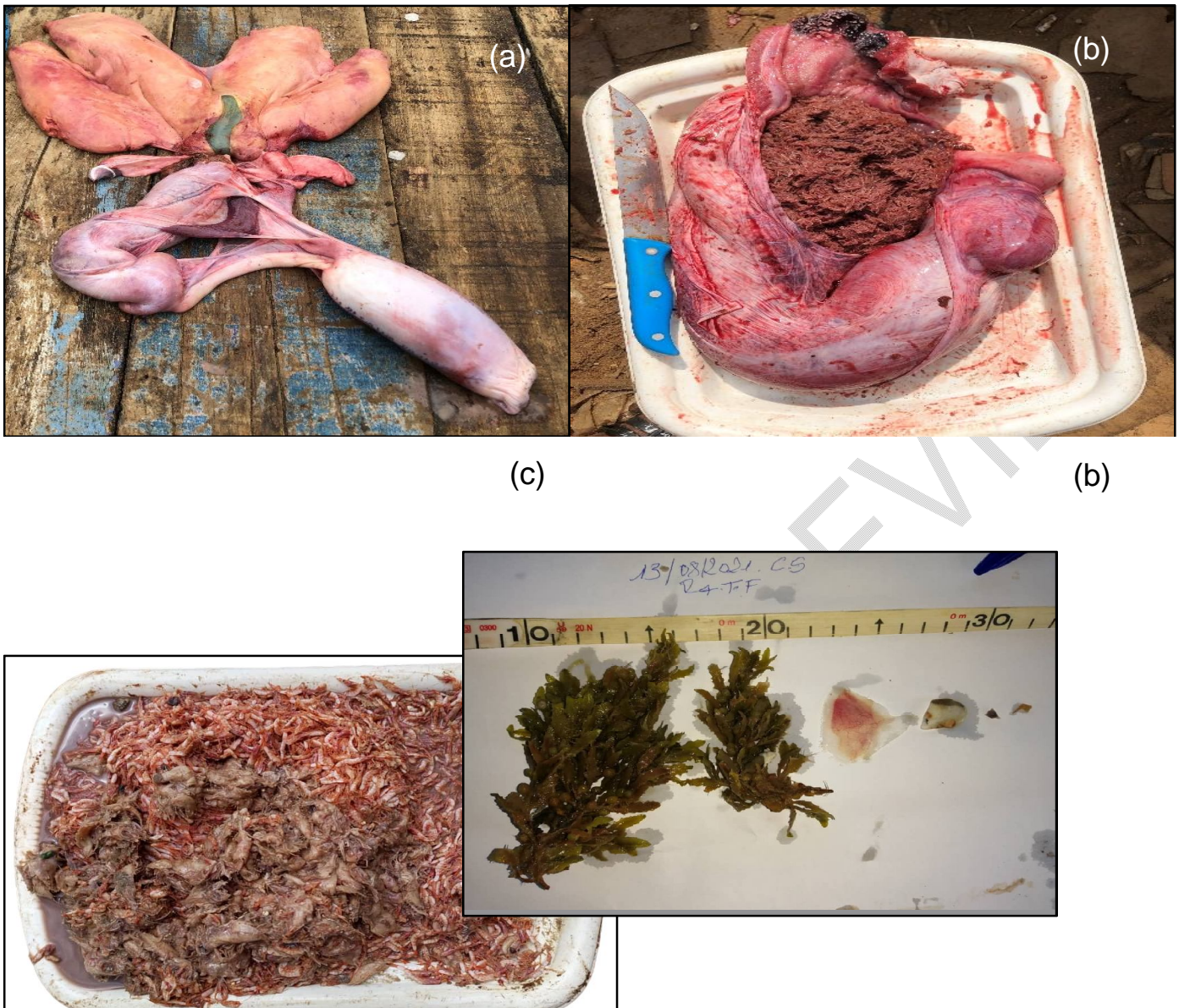


Fig. 3. Stomach contents of *Mobula tarapacana* and *Mobula japonica*. a =empty stomach in *Mobula japonica*; b =full stomach in *Mobula tarapacana*; (c and d) = stomach contents at different states of digestion, including shrimp, fish and algae .

Overall diet composition

The dietary spectrum of *M. tarapacana* included 12 prey items, belonging to 8 families which can be grouped into five major categories: crustaceans, algae, teleost fishes, molluscs and insects. The quantitative analysis of the diet showed that crustaceans (%PSIRI = 68.62%), mostly represented by *Sergestes atlanticus* (%PSIRI = 49.83) and euphausiid *Pseudeuphausia latifrons* (%PSIRI = 17.87%) were the main ingested prey of *M. Tarapacana*. These prey items were followed by the marine algae of the genus *Sargassum* (%PSIRI = 15.76%), composed of *Sargassum natans* (%PSIRI = 8.14) and *Sargassum fluitans* (%PSIRI = 7.63) and several fish species, namely *Remora remora* (%PSIRI = 2.54),

Sardinella aurita (%PSIRI = 1.81), *Trichiurus lepturus* (%PSIRI = 0.72), *Priacanthus arenatus* (%PSIRI = 0.60) and *Chloroscombrus chrysurus* (%PSIRI = 0.59). The other taxonomic groups (insects and molluscs) representing less than 5.00% of the %PSIRI were incidental food in the diet of this species (Table 1). In contrast, the food spectrum of *M. japonica* is less varied and consisted of two main categories of prey namely crustaceans and algae. Crustaceans were the most important taxonomic group in the diet (PSIRI = 94.67%), followed by prey belonging to the algae of the genus *Sargassum* (PSIRI = 5.33), in particular *S. natans* (%PSIRI= 2.00) and *S. fluitans* (%PSIRI = 3.33) which can be considered as incidental food (Table 2). Among crustaceans, *S. atlanticus* (%PSIRI = 63.33) and *P. latifrons* (%PSIRI = 31.34%) were the most important prey ingested by this species.

Table 1. General overview of the diet of *Mobula tarapacana* captured from March 2020 to December 2022 in the coastal waters of Côte d'Ivoire by the artisanal gillnet fishery. %FO = percentage frequency of occurrence; %PN = prey specific number percentage; %N= number percentages (%N); %PW= percentage of specific weight of these same prey; W = weight percentage and %PSIRI = prey-specific relative importance index; S_i = specific abundance; (ind) = indeterminate.

| Categories | Prey | %FO | %PN | %N | %PW | %W | %PSIRI | S_i | |
|--------------------|---------------------------------|--------------|-------------|--------------|-------------|--------------|--------------|-------------|-------|
| Crustaceans | | 72.88 | 2.58 | 69.76 | 2.31 | 67.47 | 68.62 | - | |
| Sergestidae | <i>Sergestes atlanticus</i> | 52.53 | 0.97 | 50.84 | 0.93 | 48.81 | 49.83 | 93.62 | |
| Euphausiidae | <i>Pseudeuphausia latifrons</i> | 18.64 | 0.95 | 17.80 | 0.96 | 17.95 | 17.87 | 99.51 | |
| Portunidae | <i>Portunus sayi</i> | 1.69 | 0.66 | 1.12 | 0.42 | 0.71 | 0.92 | 42.86 | |
| Algae | | 22.03 | 1.28 | 14.07 | 1.59 | 17.46 | 15.76 | - | |
| | <i>Sargassum natans</i> | 11.86 | 0.61 | 7.29 | 0.76 | 8.98 | 8.14 | 73.46 | |
| | <i>Sargassum fluitans</i> | 10.17 | 0.67 | 6.78 | 0.83 | 8.47 | 7.63 | 93.46 | |
| Teleosts | | 18.64 | 2.64 | 9.14 | 3.31 | 10.92 | 10.03 | - | |
| Priacanthidae | <i>Priacanthus arenatus</i> | 3.39 | 0.03 | 0.12 | 0.32 | 1.08 | 0.60 | 35.84 | Tab |
| Clupeidae | <i>Remora remora</i> | 3.39 | 0.75 | 2.54 | 0.75 | 2.54 | 2.54 | 75.00 | le 2. |
| Echeneidae | <i>Sardinella aurita</i> | 3.39 | 0.50 | 1.69 | 0.57 | 1.92 | 1.81 | 32.29 | Gen |
| Carangidae | <i>Chloroscombrus chrysurus</i> | 1.69 | 0.30 | 0.51 | 0.39 | 0.66 | 0.58 | 39.12 | eral |
| Trichiuridae | <i>Trichiurus lepturus</i> | 1.69 | 0.32 | 0.54 | 0.53 | 0.9 | 0.72 | 53.68 | over |
| | Fish (undetermined) | 5.08 | 0.73 | 3.73 | 0.75 | 3.81 | 3.77 | 48.81 | vie |
| Mollusc | | 3.39 | 0.49 | 0.83 | 0.45 | 0.76 | 0.80 | - | w of |
| Sepiidae | <i>Sepia officinalis</i> | 1.69 | 0.16 | 0.27 | 0.16 | 0.27 | 0.27 | 16.09 | the |
| Bivalves | Undetermined | 1.69 | 0.33 | 0.56 | 0.29 | 0.49 | 0.53 | 29.16 | |
| Insects | Undetermined | 6.78 | 0.92 | 6.20 | 0.50 | 3.40 | 4.80 | 2.60 | |

diet of *Mobula japonica* captured from March 2020 to December 2022 in the coastal waters of Côte d'Ivoire by the artisanal gillnet fishery. %FO = percentage frequency of occurrence; %PN = prey specific number percentage; %N =

number percentages (%N); %PW = percentage of specific weight of these same prey; W = weight percentage and %PSIRI = prey-specific relative importance index; S_i = specific abundance.

| Categories | Prey | %FO | %PN | %N | %PW | %W | %PSIRI | Si |
|--------------------|---------------------------------|--------------|--------------|-------------|--------------|-------------|--------------|--------|
| Crustaceans | | 94.99 | 94.99 | 2.00 | 94.36 | 1.99 | 94.67 | - |
| | <i>Sergestes atlanticus</i> | 63.33 | 63.33 | 1.00 | 63.33 | 1.00 | 63.33 | 100.00 |
| | <i>Pseudeuphausia latifrons</i> | 31.66 | 31.66 | 1.00 | 31.03 | 0.99 | 31.34 | 97.70 |
| Algae | | 6.66 | 5.01 | 1.58 | 5.63 | 1.69 | 5.33 | - |
| | <i>Sargassum natans</i> | 3.33 | 1.69 | 0.58 | 2.30 | 0.69 | 2.00 | 86.42 |
| | <i>Sargassum fluitans</i> | 3.33 | 3.33 | 1.00 | 3.33 | 1.00 | 3.33 | 100.00 |

Diet in relation to fish size and marine seasons

Fish were grouped into two categories: juvenile individuals (n = 59) with sizes of 154–256 cm, DW and adults (n = 157) with sizes of 257–371 cm, DW for *M. tarapacana*. In *M. japonica*, sizes of juveniles (n = 32) ranged between 80–177 cm DW while adults (n = 178) ranged in sizes of 177–369 cm DW. For *M. tarapacana*, the trophic spectrum of juveniles consisted of crustaceans, in particular *S. atlanticus* (%PSIRI = 50) and *P. latifrons* (%PSIRI = 50), whilst the diet of adults was more diversified, including crustaceans (%PSIRI = 62.95), algae (%PSIRI = 21.12), teleost fishes (%PSIRI = 9.18), insects (%PSIRI = 5.81) and molluscs (%PSIRI = 0.93) (Table 3). For *M. japonica*, the juveniles as well as adults consumed mainly crustaceans (PSIRI = 100% for juveniles and 94.64% for adults), followed by the algae of the genus *Sargassum* (PSIRI = 5.36) in adult individuals (Table 4). The Morisita-Horn index indicated a high trophic overlap between size groups for *M. tarapacana* ($C\lambda = 0.766$) and *M. japonica* ($C\lambda = 0.939$), indicating that both species preferentially feed on the same preys.

The Spearman test showed a strong similarity between the diet of adults and juveniles in *M. tarapacana* (N = 59; $R_s = 0.89$; $p < 0.05$) and a moderate similarity in *M. japonica* (N = 60; $R_s = 0.59$; $p < 0.05$), indicating that the two size groups in both species exploit the same types of resources.

As for marine seasons, the prey was similar in both seasons, but the proportions varied considerably (Table 3). During the cold season, the trophic spectrum of *M. tarapacana* consisted mainly of *S. atlanticus* (%PSIRI = 41.16), *P. latifrons* (%PSIRI = 19.05), *S. natans* (%PSIRI = 8.82%), *R. remora* (%PSIRI = 7.14), fish remains (%PSIRI = 4.76) and *S. fluitans* (%PSIRI = 2.31). The same prey items were found in the warm season, with variations in the order of importance: *S. atlanticus* (%PSIRI = 54.84), *P. latifrons* (%PSIRI = 17.88), *S. natans* (%PSIRI = 8.03%), *S. fluitans* (%PSIRI = 9.49), *S. aurita* (%PSIRI = 3.08) and fish remains (%PSIRI = 3.23). The other teleost families and molluscs were incidental

foods. Concerning *M. japonica*, crustaceans including *S. atlanticus* and *P. latifrons* represented 100% of the PSIRI in warm season (Table 4). During this season, *S. atlanticus* (%PSIRI = 66.67) was the preferential prey, while *P. latifrons* (%PSIRI=33.33%) was eaten as secondary prey. In cold seasons (n = 47), apart *S. atlanticus* and *P. latifrons* which constituted 63.83% and 31.53% of the %PSIRI, the algae of the genus *Sargassum* were lightly encountered in stomachs (%PSIRI = 4.64). The Morisita-Horn indices calculated separately for *M. japonica* ($C\lambda = 0.997$) and *M. tarapacana* ($C\lambda = 0.95$) indicated a high level of trophic overlap between the warm and cold seasons even if no significant difference was observed in diet. The Spearman test revealed a moderate similarity between the diets of *M. tarapacana* (N= 59; $R_s = 0.35$; $p < 0.05$) and a strong similarity for *M. japonica* (N = 59; $R_s = 0.94$; $p < 0.05$), indicating that both species exploit the same types of food resources in all seasons.

Table 3. Diet composition based on sex, marine seasons and size class groups of *Mobula tarapacana* captured from April 2020 to May 2022 in the coastal waters of Côte d'Ivoire.

| Item prey | Prey-specific relative importance index (%PSIRI) | | | | | |
|----------------------------------|--|--------------|--------------|--------------|---------------|--------------|
| | Males | Females | Cold | Warm | Juveniles | Adults |
| Crustaceans | 65.42 | 73.92 | 60.21 | 74.15 | 100.00 | 62.95 |
| <i>Sergestes. atlanticus</i> | 47.29 | 52.88 | 41.16 | 54.84 | 50.00 | 50.71 |
| <i>Pseudeuphausia. Latifrons</i> | 16.57 | 21.04 | 19.05 | 17.88 | 50.00 | 10.20 |
| <i>Portunus sayi</i> | 1.56 | 0.00 | 0.00 | 1.43 | 0.00 | 2.04 |
| Algae | 20.57 | 9.59 | 11.13 | 17.52 | 0.00 | 21.12 |
| <i>Sargassum natans</i> | 8.64 | 5.42 | 8.82 | 8.03 | 0.00 | 12.96 |
| <i>Sargassum fluitans</i> | 11.93 | 4.17 | 2.31 | 9.49 | 0.00 | 8.16 |
| Teleosts | 6.87 | 13.23 | 13.6 | 7.96 | 0.00 | 9.18 |
| <i>Priacanthus arenatus</i> | 0.64 | 0.46 | 1.69 | 0.00 | 0.00 | 0.73 |
| <i>Remora remora</i> | 0.00 | 6.25 | 7.14 | 0.00 | 0.00 | 2.04 |
| <i>Sardinella aureta</i> | 2.55 | 0.00 | 0.00 | 3.08 | 0.00 | 0.58 |
| <i>Chloroscombrus chrysurus</i> | 0.00 | 1.46 | 0.00 | 0.89 | 0.00 | 0.71 |
| <i>Trichiurus lepturus</i> | 0.82 | 0.00 | 0.00 | 0.76 | 0.00 | 0.59 |
| Fish (undetermined) | 2.86 | 5.06 | 4.76 | 3.23 | 0.00 | 4.54 |
| Molluscs | 0.00 | 1.87 | 1.47 | 0.38 | 0.00 | 0.93 |
| <i>Sepia officinalis</i> | 0.00 | 0.58 | 0.00 | 0.00 | 0.00 | 0.29 |
| Bivalves | 0.00 | 1.29 | 1.47 | 0.38 | 0.00 | 0.63 |
| Insect (undetermined) | 7.14 | 1.39 | 13.59 | 0.00 | 0.00 | 5.81 |

Table 4. Diet composition according to marine seasons and size class groups of *Mobula japonica* captured from April 2019 to May 2021 in the coastal waters of Côte d'Ivoire.

| Item prey | Prey-specific relative importance index (%PSIRI) | | | | Feeding strategy |
|---------------------------------|--|---------------|---------------|--------------|------------------|
| | Cold | Warm | Juveniles | Adults | |
| Crustaceans | 95.36 | 100.00 | 100.00 | 94.64 | The modified |
| <i>Sergestes atlanticus</i> | 63.83 | 66.67 | 50 | 64.29 | |
| <i>Pseudeuphausia latifrons</i> | 31.53 | 33.33 | 50 | 30.36 | |
| Algae | 4.64 | 0.00 | 0.00 | 5.36 | |
| <i>Sargassum natans</i> | 2.51 | 0.00 | 0.00 | 1.79 | |
| <i>Sargassum fluitans</i> | 2.13 | 0.00 | 0.00 | 3.57 | |

Costello Diagram constructed (Fig. 4) established crustaceans, in particular, *S. atlanticus* and *P. latifrons* as the main food item of both species in the coastal waters of Côte d'Ivoire. In other words, these two species display specialist feeding behaviour that focuses on *S. atlanticus* and *P. latifrons*. These species appeared in the upper right area of the diagram, whereas most of the other prey species are located in the left corner or close to the vertical axis, indicating low values for prey importance. These low frequency values suggest that almost all the other species are rare or unimportant prey and are therefore consumed by few individuals.

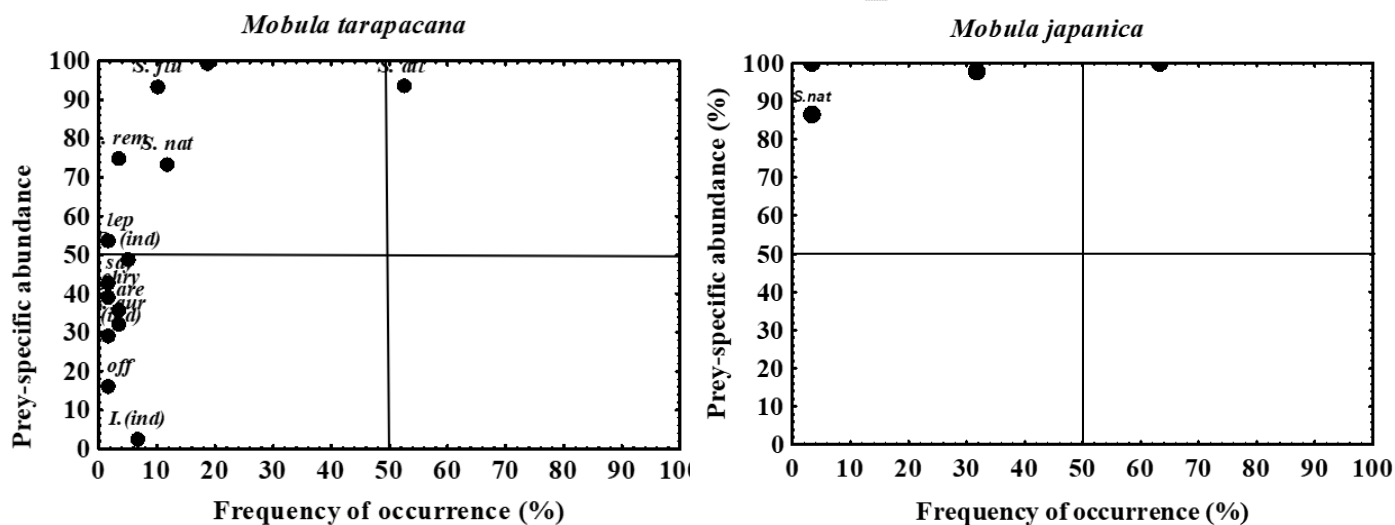


Figure 4. Costello Diagram modified by Amundsen et al. [24] described feeding strategy and niche width of *Mobula tarapacana* and *Mobula japonica* from the coastal waters of Côte d'Ivoire. The points represent different prey types in the stomach contents. *Sergestes atlanticus* (*S. atl*), *Pseudeuphausia latifrons* (*P. lat*), *Portunus sayi* (*P. say*), *Sargassum natans* (*S. nat*), *Sargassum fluitans* (*S. fl*), *Priacanthus arenatus* (*P. are*), *Remora remora* (*R. rem*), *Sardinella aureta* (*S. aur*), *Chloroscombrus chrysurus* (*C. chr*), *Trichiurus lepturus* (*T. lep*), *Sepia officinalis* (*S. off*), Insects undetermined (*I. und*) Bivalves undetermined (*B. und*).

DISCUSSION

Index of vacuity

The value of the vacuity index obtained in this study was very high (over 70%) for both species, indicating that these species can be included in the category of relatively low-feeding species. The high number of empty stomachs is thought to be due to several factors, one of which is the availability of food in nature. The prey eaten by both species were shrimps, which have the characteristic of being digested quickly. In fact, all stages of digestion were observed in the stomachs, although most of them were in an advanced or well-digested state. In addition, Shibuya et al. [26] stated that the high empty stomach could be caused by the fishing time that is not following the activities of fish that are looking for food. Fahira et al. [27] obtained similar void indices (76.2%) in *Mobula mobular*, considered conspecific with *M. japonica*. In contrast, Shirlamaine [28] reported a very low void rate in *M. japonica* from Butuan Bay, Philippines, as all stomachs examined contained prey. The high proportion of empty stomachs appears to be common to *M. tarapacana*. Indeed, Notarbatolo di Sciara [29] reported that almost all stomachs examined in this species were empty and that only traces of food were found in the folds of the stomach epithelium. Globally, this high incidence of empty stomachs may also reflect a long delay between capture and examination. In fact, the duration of the tide was 4–5 days and the fishing activities took place at night, with sets were performed at 17h00, captures occurred habitually between 00h00 and 05h00 and landings occur between 07h00 and 16h00. These results would suggest that most of specimens had fed at least 10 hours before being captured. On the other hand, the hooks used in association to driftnet by fishermen to attract rays cause high stress at the time of capture often resulting in the regurgitation of stomach contents or the whole stomach of several individuals during the data collection. This vomiting reflex is a protective mechanism for the bulk ejection of noxious material which is common in vertebrates [30]. According to Croll et al. [31], rays move to deeper waters at night to feed. Since captures usually occur at night, we assumed that several specimens were caught with empty stomachs; this may result in a higher frequency of empty stomachs.

Diet composition

The diet composition of *M. tarapacana* is more diverse, consisting of crustaceans (68.62%), algae of the genus *Sargassum*, teleost fishes, molluscs and insects. On the other hand, the dietary spectrum of *M. japonica* is essentially made up of crustaceans (94.70%) and algae of the genus *Sargassum*. As we can see, both species had a diet based mainly on crustaceans. Stevens [32] noted that in the East Atlantic areas of the Indian Ocean, *M. tarapacana* appear to be specialized in catching small fish, whereas *M. japonica* feeds mainly on zooplankton and micronectonic crustaceans such as euphausiid *P. latifrons* and sergestid shrimps *Acetes intermedius* and *Lucifer* spp., copepods and other rare prey items [14-28]. This suggests that the prey dominance in the diet varies according to space and their abundance in the environment [33]. Based on the quantitative analysis of the diet through the %PSIRI, the diet of both species was made up mainly of crustaceans, in particular the Shrimp *S. atlanticus* and *P. latifrons*. Their importance in the diet of these Mobulid

species could be due to their abundance in the environment, as [34] reported high concentrations of shrimp along the coast of Côte d'Ivoire. The presence of teleost fishes, crabs, molluscs, cephalopods and insects attests the ability of *M. tarapacana* to adjust its diet according to the availability of some preys, relying on seasonal variations or environmental conditions to optimise its diet. Some previous studies carried out on *M. japonica* reported a low diversity of ingested prey composed exclusively of pelagic crustaceans such as euphausiids and other zooplankton species [1,13,14,28]. Two algae of the genus *Sargassum* (*S. natans* and *S. fluitans*) which seasonally invade marine waters [35] were identified in stomachs. The hypothesis that could explain the presence of algae in stomachs is linked to the Mobulid's hunting and predation strategy, which seems to be closely linked to the way they take food, by propelling themselves to capture small schooling fish (Stevens [29]) or by extracting prey buried in the carpet formed by this algae [36-37]. According to Coston-Clements et al.[38], *Sargassum* is a group of brown algae that provides food, refuge, and breeding ground for many marine animals, such as turtles, crabs, shrimp, fish, and seabirds. In this condition, they can be considered as incidental items. The presence of the shrimps (*S. atlanticus* and *P. latifrons*) and the crab *Portunus sayi* indicated that this species migrates between pelagic and benthic zones.

Diet in relation to fish size and marine seasons

The feeding habits of both species did not change significantly according seasons and the Morisita-Horn index 0.997 (*M. japonica*) and 0.950 (*M. tarapacana*) indicated a similarity of diet. However, the proportions and relative importance of each prey type vary. Thus, the diet was richer in the cold season, due to variations in the abundance of groups of benthic and pelagic fauna constituting the majority of prey. This study also showed ontogenetic variations in the feeding habits of both species. In fact, the trophic spectrum of juveniles consisted of crustaceans (essentially *S. atlanticus* and *P. latifrons*), whilst that of adults was more diversified, including in addition to crustaceans, algae, teleost fishes, insects and molluscs. As we can see, as fish sizes increase, they gradually add other prey to their diet. This is consistent with Jacobsen and Bennett [33], who found that the diet of rays varies depending on body size, morphology, and sexual maturity status. Varghese et al. [39], reported that prey diversity in the adult diet could also be associated with the increase of energy requirements that increases with fish sizes.

Food strategy

The feeding strategy involves supplementing the diet with more mobile, calorie-rich prey; reducing the time spent foraging and devoting the energy gained to reproductive activity. The Costello diagram indicates that these *Mobula* species are selective predators or specialise in eating shrimp species throughout the year. The feeding strategy of *M. tarapacana* and *M. japonica* shows a strong affinity for the shrimps *S. atlanticus* and *P. latifron*. Indeed, rays in general, show a strong preference for planktonic organisms, adapted to the morphology of their gills [40]. Thus, the predatory instinct of these

species pushes them to target mainly slow prey, abundant in the environment and adapted to the morphology of the gill plates. In addition, *M. tarapacana* also consumes larger prey, such as teleosts thanks to its large gill filter allowing a greater trophic diversity than *M. japonica*. The presence of fish such as *Trichiurus lepturus* and other species of 10 to 39 cm long suggests an ability of this species to capture dense prey. From an energetic point of view, it is plausible that *M. tarapacana* and *M. japonica* migrate to the Ivorian coast to feed during periods of high zooplankton biomass, regardless of taxonomic composition or prey size. Since both species efficiently exploit the same food resources, interspecific and intraspecific competition is to be expected between these two species, which are closely related taxonomically and ecologically. Although *M. japonica* and *M. tarapacana* share the same habitat in Ivorian ZEE, however, habitat use differed with seasons and peaks in abundance, a reduction in available resources could increase competition.

4. CONCLUSION

Through this study, original results were obtained concerning the diet of these species of Mobulids. Both species feed mainly on benthic shrimps of the Sergestidae and Euphausiidae families. However, the diet of *M. tarapacana* is more diversified, including fish, Cephalopods, Crabs, Insects and Bivalves. Two algae of the genus *Sargassum* (*S. natans* and *S. fluitans*) were identified in stomachs, indicating that, these species hunt their prey by extracting prey buried in the mat formed by these algae. These species can be considered as carnivorous predators targeting shrimp species. These current results provide a useful contribution to the local conservation and management of Mobulids in Côte d'Ivoire.

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ETHICAL APPROVAL

Fish sampling methodology was approved via the Ministry in charge of Ministry of Animal Resources and Fisheries.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Authors hereby declare that no generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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