

Feeding Ecology and Diet Composition of *Solea solea* (Linnaeus, 1758) in Oran Bay, Western Algeria

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ABSTRACT

This study investigated the feeding ecology of the common sole *Solea solea* (Linnaeus, 1758) in Oran Bay, western Algeria. A total of 360 specimens (210 females, 150 males; total length: 10.1-30.0 cm, 19.47 ± 5.84 cm; body weight: 8.85-248.39 g, 79.77 ± 61.90 g) were obtained monthly from commercial trawl landings between January and December 2024, with 21-36 individuals per month. Biometric data assigned 192 individuals to $TL < 20$ cm and 168 to $TL \geq 20$ cm. Stomach contents were analyzed using the vacuity coefficient and quantitative diet indices (F%, Cn%, Cp%, Q, IA and IRI). Of 360 stomachs, 162 were empty and 198 non-empty; diet indices used non-empty stomachs as denominators. The overall vacuity coefficient was 45%, higher in females than males (48.57% vs. 40.00%) but not significant ($\chi^2 = 2.60$, $df = 1$, $p = 0.107$). In females, monthly Cv% and GSI% were negatively correlated ($n = 12$, $r = -0.953$, $df = 10$, $p < 0.001$), suggesting a link between feeding activity and reproduction. A total of 512 prey items were recorded, including identified and unidentified prey categories but excluding organic debris, sediment particles, and plant material; based on 198 non-empty stomachs, this corresponds to an average of 2.59 prey items per non-empty stomach. The diet consisted mainly of benthic invertebrates, with crustaceans and polychaetes as the most important dietary components. Because prey availability and benthic macrofauna were not sampled, these findings reflect stomach-content importance rather than true prey preference. Seasonal differences in numerical diet composition were not significant (Pearson $\chi^2 = 12.15$, $df = 18$, $p = 0.840$; G-test: $G = 12.61$, $df = 18$, $p = 0.814$). Overall, diet composition is consistent with an opportunistic benthic feeding strategy and provides baseline trophic information, without directly evaluating stock status, fishing pressure or management scenarios.

INTRODUCTION

Understanding fish feeding ecology is essential for properly interpreting the ecological role of species within marine ecosystems and for developing effective fisheries management and conservation strategies (Koné, 2007). Notably, trophic studies constitute a fundamental tool in marine ecology, as they provide detailed information on prey availability, energy transfer mechanisms, and interspecific interactions that structure aquatic food webs (Hajisamae, 2003). These approaches are particularly important in dynamic coastal environments where food resources and environmental conditions can vary significantly over space and time.

Among benthic fish species, *Solea solea* (Linnaeus, 1758) is recognized as one of the most ecologically and economically important flatfish in the Mediterranean Sea and the eastern Atlantic coastal waters. This species typically inhabits sandy and muddy bottoms, where it adopts a demersal lifestyle closely linked to the seabed. Its diet is mainly composed of benthic invertebrates, including polychaete worms, crustaceans, molluscs, and various small organisms associated with soft-bottom habitats (Fischer *et al.*, 1987). However, its feeding ecology is not static, as numerous studies have shown that dietary composition can fluctuate in response to environmental and biological factors such as seasonality, habitat structure, prey abundance, and individual size classes (Cabral, 2000; Amara *et al.*, 2001). This variability highlights the adaptability of the species to changing environmental conditions.

Solea solea is widely considered an opportunistic benthophagous predator characterized by a high degree of trophic flexibility. This feeding strategy allows it to exploit a wide range of prey types depending on their availability in the environment. In addition, ontogenetic shifts in diet have been frequently reported, indicating that feeding habits evolve throughout the life cycle of the species. Juvenile individuals tend to consume smaller and more easily accessible prey, whereas larger adults progressively shift toward a more diversified diet that may include larger benthic organisms. This ontogenetic plasticity plays an important role in reducing intraspecific competition and enhancing survival across different developmental stages.

Oran Bay, located along the western Algerian coast, is characterized by a mosaic of soft-bottom habitats, including sandy and muddy substrates that support benthic invertebrate communities typical of Mediterranean coastal ecosystems. Previous benthic surveys along the Algerian coast have shown that fine sand communities occupy a comparatively limited surface area within Oran Bay relative to other Algerian bays, reflecting the specific sedimentary and hydrodynamic conditions of this semi-enclosed system (Bakalem *et al.*, 2009). The bay also supports an active artisanal and small-scale commercial fishery, in which flatfish such as *Solea solea* represent a valued component of local landings. In addition, Oran Bay has been repeatedly used as a study site for biomonitoring of benthic fish species, including assessments of trace metal contamination in *Solea solea* (Tabeche *et al.*, 2021) and in other benthic species such as *Mullus barbatus* Linnaeus, 1758 (Lakmeche *et al.*, 2025), underscoring both the ecological relevance of this area and the need for complementary trophic ecology data.

In Algeria, despite its ecological importance, research on the trophic ecology of *Solea solea* remains relatively limited, particularly along the western coastline. In particular, annual and seasonal diet data, information on ontogenetic (size-related) shifts in prey composition, and data linking feeding activity to the reproductive cycle are currently lacking for this region, which represents a gap in understanding the functioning of coastal food webs. Moreover, *Solea solea* has also been identified as a relevant bioindicator species for monitoring trace metal contamination in western Algerian coastal waters (Tabeche *et al.*, 2021), which further emphasizes its ecological significance in environmental assessment studies. In this context, the present study aims to provide a quantitative analysis of the diet composition of *Solea solea* in Oran Bay through stomach content analysis, with particular emphasis on the relative importance of different prey categories and their variation according to seasonal dynamics and biological characteristics of the species.

MATERIALS AND METHODS

Sample Collection

Specimens of *Solea solea* were obtained monthly from commercial trawl catches landed in Oran Bay, western Algeria (35.8239°N, 0.4132°W), over a one-year period, from January 2024 to December 2024 (21-36 individuals per month). Precise fishing depth and substrate type were not documented, as samples originated from commercial landings rather than dedicated research surveys. The study area is shown in Fig. (1).

A total of 360 individuals were analyzed, comprising 210 females and 150 males. Monthly sample sizes ranged from 21 to 36 individuals, with sex ratios and size-class distributions ($TL \geq 20$ cm and $TL < 20$ cm) presented in Table (1). The total length of the sampled fish ranged from 10.1 to 30 cm. Biometric values were as follows: total length: 10.1–30.0 cm, 19.47 ± 5.84 cm; body weight: 8.85–248.39 g, 79.77 ± 61.90 g. Each specimen was measured to the nearest millimeter and weighed to the nearest gram. Sex was determined by macroscopic examination of the gonads (based on their color, size, and morphology) during dissection, and this method proved reliable even for individuals smaller than 20 cm TL. No numerical maturity scale was applied. Instead, individuals were classified into two size classes ($TL \geq 20$ cm and $TL < 20$ cm) to distinguish large-sized from small-sized individuals, based on the reported first-year growth size of *Solea solea* in the Mediterranean (18–20 cm TL; Shéhata, 1984).

Following dissection, stomachs were extracted and weighed fresh (prior to fixation) to determine stomach content weight. They were then immediately preserved in a 10% formalin solution to inhibit enzymatic activity and ensure adequate preservation of prey items for subsequent taxonomic identification. As weighing was performed before fixation, Cp% values were calculated based on fresh weights, thus avoiding potential bias associated with formalin-induced weight alteration.

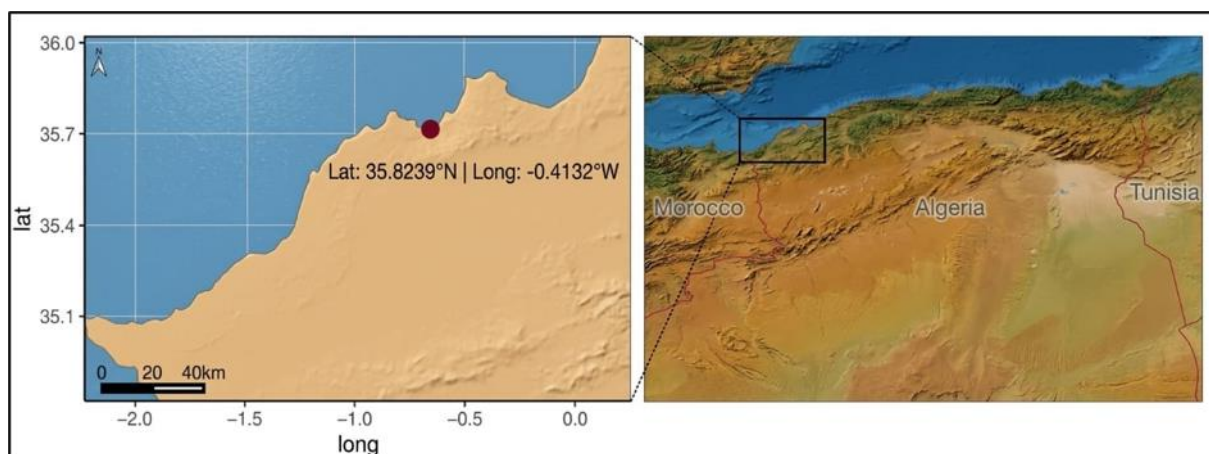


Fig. 1. Location of the study area: Oran Bay (Tabèche *et al.*, 2021).

Stomach Content Analysis

Each stomach was dissected longitudinally, and the contents were carefully transferred into Petri dishes for analysis under a stereomicroscope, at magnifications ranging from $\times 10$ to $\times 40$ depending on the degree of fragmentation and the taxonomic group examined. Identification was carried out using specialized taxonomic keys and reference guides for each prey group: polychaetes were identified following Fauvel (1923, 1927) and Hayward and Ryland (1995); crustaceans following Zariquiey Álvarez (1968) and Ingle (1980); molluscs following Poppe and Goto (1991, 1993); and ascidians following Monniot and Monniot (1972). Nematodes could generally only be identified to the phylum level, given their advanced state of digestion and the lack of specific taxonomic keys applicable to stomach content material. All prey items were subsequently sorted, identified, counted, and weighed.

When digestion was too advanced to allow precise taxonomic identification, remains were grouped into broader taxonomic categories to ensure consistent and reliable classification of the stomach contents. In such cases, fragments or remains belonging to the same prey item were counted as a single individual, regardless of the degree of fragmentation, in order to avoid overestimating prey abundance. Similarly, the total weight of all fragments or remains attributed to the same prey item was recorded as the weight of that single individual, following the same logic applied to counting.

Quantitative Analysis of Diet

The quantitative approach provides a better understanding of the relative contribution of each prey category to the overall diet and allows the detection of potential variations in feeding strategies (Quinius, 1978). In this study, several trophic indices were applied to characterize the feeding ecology of *Solea solea*.

To better evaluate the trophic importance of each prey category, the vacuity coefficient (Cv%) was first calculated using all stomachs examined. Calculations for the frequency of occurrence (F%), numerical percentage (Cn%), weight percentage (Cp%), Hureau's feeding coefficient (Q), Lauzanne's alimentary index (IA), and the index of relative importance (IRI) were then performed using only non-empty stomachs. In addition, Levin's standardized niche breadth index (Bsta) and the Shannon diversity index (H') were calculated based on the numerical proportions (Cn%) of prey categories to assess trophic niche breadth and diet diversity, respectively.

(1) The vacuity coefficient: was calculated as:

$$Cv\% = N_v/N_t \times 100$$

Where, N_v is the number of empty stomachs and N_t is the total number of stomachs examined.

(2) The frequency of occurrence: was calculated as:

$$F\% = N_i/N \times 100$$

Where, N_i is the number of non-empty stomachs containing prey i , and N is the total number of non-empty stomachs.

(3) The numerical percentage: was calculated as:

$$Cn\% = (n_i/N_{total}) \times 100$$

Where, n_i is the number of individuals of prey i , and N_{total} is the total number of prey items.

(4) **The weight percentage:** was calculated as:

$$Cp\% = Wi/W_{total} \times 100$$

Where, W_i is the weight of prey i , and W_{total} is the total weight of all prey items.

(5) **Hureau's feeding coefficient (Hureau, 1970):** Is defined as the product of numerical and weight contributions, allowing the identification of dominant prey types: $Q = Cn\% \times Cp\%$

(6) **Lauzanne's alimentary index (Lauzanne, 1975):** Integrates both occurrence and biomass:

$$IA = (F\% \times Cp\%) / 100$$

(7) **The index of relative importance (Pinkas *et al.*, 1971):** Combines frequency, numerical abundance, and weight to provide an integrated measure of prey importance:

$$IRI = F\% \times (Cn\% + Cp\%)$$

(8) **Levin's standardized niche breadth index (Levins, 1968):** was calculated as:

$$B_{sta} = (B - 1) / (n - 1)$$

Where, $B = 1 / \sum p_i^2$, and p_i is the proportion of prey category i in the diet (based on $Cn\%$), and n is the number of prey categories.

(9) **The Shannon diversity index (Shannon, 1948):** was calculated as: $H' = - \sum p_i \ln(p_i)$

Where, p_i is the proportion of prey category i in the diet (based on $Cn\%$).

Feeding Activity and Basic Indices

The vacuity coefficient ($Cv\%$) represents the proportion of empty stomachs relative to the total number of examined individuals (Santić *et al.*, 2003), and was used as an indicator of feeding intensity.

The frequency of occurrence ($F\%$) expresses the proportion of stomachs containing a given prey type relative to all non-empty stomachs (Rosecchi & Nouaze, 1985). This index highlights the regularity of consumption of each prey category.

The numerical percentage ($Cn\%$) reflects the relative abundance of each prey type based on counts, whereas the weight percentage ($Cp\%$) indicates their proportional contribution by biomass. All prey items were blotted superficially with absorbent paper to remove excess surface moisture prior to weighing, and were weighed to the nearest 0.001 g on an analytical balance. Weights correspond to wet weight.

Statistical analysis

A chi-square test of independence was used to compare the vacuity coefficient ($Cv\%$) between female and male *Solea solea*, based on individual stomach fullness data (empty vs. full). A Pearson correlation analysis was performed to assess the relationship between monthly vacuity coefficient ($Cv\%$) and gonadosomatic index ($GSI\%$) values in female *Solea solea*, based on the twelve monthly values recorded over the study period. A contingency analysis (Pearson chi-square test and likelihood-ratio G-test) was performed to assess seasonal differences in the numerical composition of the diet, using prey counts by season and prey category. All statistical analyses were performed using IBM SPSS Statistics version 25 (IBM Corp., Armonk, NY, USA). Statistical significance was set at $\alpha = 0.05$ for all analyses.

RESULTS

Qualitative Analysis of Diet

Inventory of Stomach Contents

Fish species do not feed on the same types of prey, and these differences are generally reflected in their anatomical characteristics, particularly the morphology of the mouth and digestive tract, which are closely related to feeding behavior.

Solea solea is a benthic teleost fish inhabiting sandy and muddy coastal bottoms, where it feeds mainly on benthic invertebrates (Fischer *et al.*, 1987). The present study focuses on the analysis of the diet of this species from Oran Bay using both qualitative and quantitative approaches, including the vacuity coefficient and several feeding indices.

The examination of stomach contents allowed the identification of the different prey categories consumed by *Solea solea*. However, due to advanced digestion of certain prey items, precise identification was sometimes impossible, and some organisms were classified at higher taxonomic levels. A total of 512 prey items were recorded, belonging to five major phyla (Annelida, Arthropoda, Mollusca, Nematoda, and Chordata) and several zoological classes, including Polychaeta, Malacostraca, Bivalvia, Gastropoda and Ascidiacea. This prey diversity is presented in Table (1).

The qualitative analysis revealed the frequent presence of polychaetes, crustaceans, molluscs, nematodes, and ascidians in the stomach contents, confirming the benthic feeding habit of the species and its exploitation of a wide range of invertebrate fauna associated with sandy and muddy substrates. Organic debris, sediment particles, and plant material were also frequently observed in several stomachs examined; although these elements were not considered prey items and were excluded from the dietary indices, their frequent occurrence is ecologically relevant, reflecting the close association of this benthic flatfish with the sediment-substrate interface during foraging.

Table 1. Faunistic inventory of prey ingested by *Solea solea* from Oran Bay.

Phylum	Class	Major prey group	Genus and species
Annelida	Polychaeta	Polychaetes	<i>Hediste diversicolor</i> , <i>Capitella capitata</i>
Arthropoda	Malacostraca	Crustaceans	<i>Crangon crangon</i> , <i>Gammarus</i> sp., <i>Eurydice pulchra</i>
Mollusca	Bivalvia	Bivalves	<i>Donax trunculus</i> , <i>Macomangulus tenuis</i>
	Gastropoda	Gastropods	<i>Tritia reticulata</i>
Nematoda	-	Nematodes	Unidentified nematodes
Chordata	Ascidiacea	Ascidians	Unidentified ascidians

Note. Taxonomic nomenclature follows the World Register of Marine Species (WoRMS, 2026).

Quantitative Analysis of Diet

To investigate the quantitative aspect of the diet, several trophic indices were calculated, including the vacuity coefficient (Cv), frequency of occurrence (F%), numerical percentage (Cn%), weight percentage (Cp%), feeding coefficient (Q), alimentary index (IA), and index of relative importance (IRI).

Vacuity Coefficient (Cv%)

The analysis of stomach contents of *Solea solea* involved a total of 360 stomachs. Among these, 198 stomachs were full (55%), while 162 stomachs were empty, representing 45% of the total

examined. The overall vacuity coefficient was therefore estimated at 45% (Fig. 2). The distribution of full and empty stomachs according to sex, season, and size class is presented in Table (2).

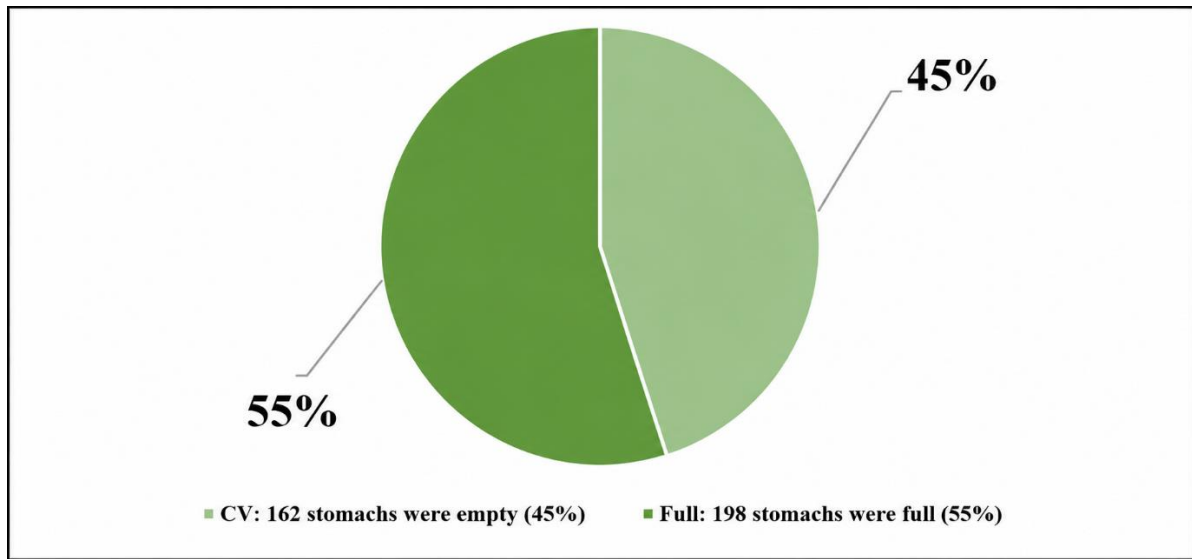


Fig. 2. Overall vacuity coefficient (Cv%) of *Solea solea* from Oran Bay.

Table 2. Distribution of full and empty stomachs of *Solea solea* from Oran Bay according to sex, season, and size class.

Stomach Status	Number	Percentage (%)	Sex		Season				Size (cm)	
			Female	Male	Winter	Spring	Summer	Autumn	TL < 20	TL ≥ 20
Full stomach	198	55 %	108	90	52	58	41	47	119	79
Empty stomach (CV)	162	45 %	102	60	22	35	62	43	73	89
Total	360	100 %	210	150	74	93	103	90	192	168

Variation of the Vacuity Coefficient (Cv%) According to Sex

The analysis of the vacuity coefficient according to sex revealed differences between females and males of *Solea solea* from Oran Bay (Fig. 3). Females exhibited a higher vacuity coefficient (48.57%) compared to males (40.00%). A chi-square test of independence, based on individual stomach fullness data, showed that this difference was not statistically significant ($\chi^2 = 2.60$, $df = 1$, $p = 0.107$; Table 3). Therefore, no significant sex-based difference in feeding intensity could be established for this population.

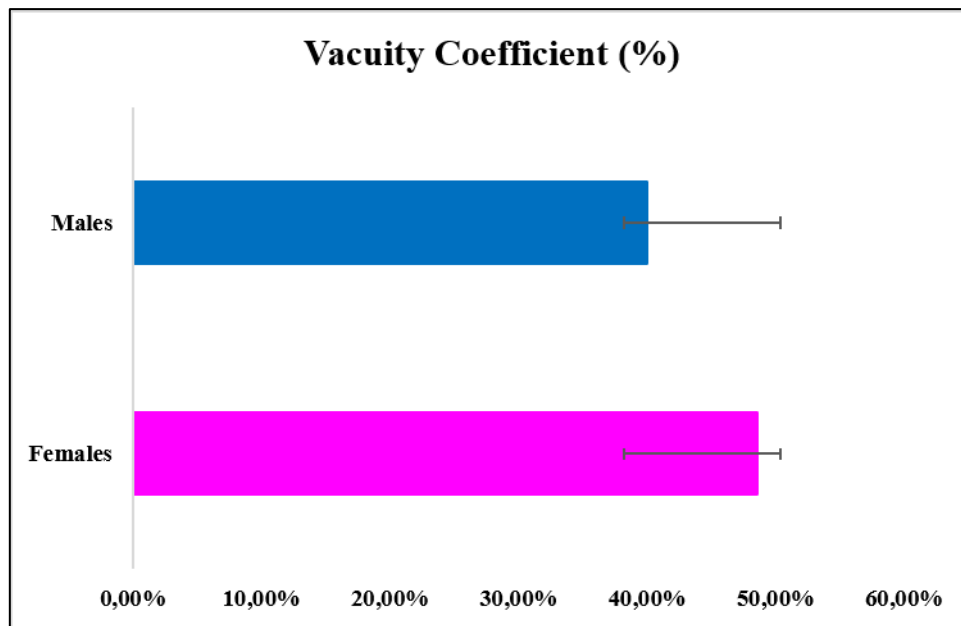


Fig. 3. Vacuity coefficient (Cv%) according to sex in *Solea solea* from Oran Bay.

Table 3. Comparison of vacuity coefficient (Cv%) between female and male *Solea solea* from the Bay of Oran using a chi-square test.

Sex	n	Empty stomachs	Full stomachs	Cv%	χ^2	df	p-value
Female	210	102	108	48.57	2.60	1	0.107
Male	150	60	90	40.00			
Total	360	162	198	45.00			

Note. n = number of individuals.

The monthly variation of the vacuity coefficient also showed fluctuations throughout the year in both sexes, with monthly sample sizes provided in Table (4). In females, the highest Cv% values were recorded during July (68.42%, n = 22) and August (72.15%, n = 18), whereas the lowest value was observed in February (28.57%, n = 14). In males, the maximum vacuity coefficient was observed in August (61.33%, n = 18), while the minimum value was recorded in January (24%, n = 8). As monthly sample sizes ranged from 8 to 23 individuals per sex, these percentages should be interpreted with some caution, particularly for months with the smallest sample sizes. These monthly variations indicate seasonal changes in feeding activity, probably associated with reproductive cycle and environmental conditions (Fig. 4).

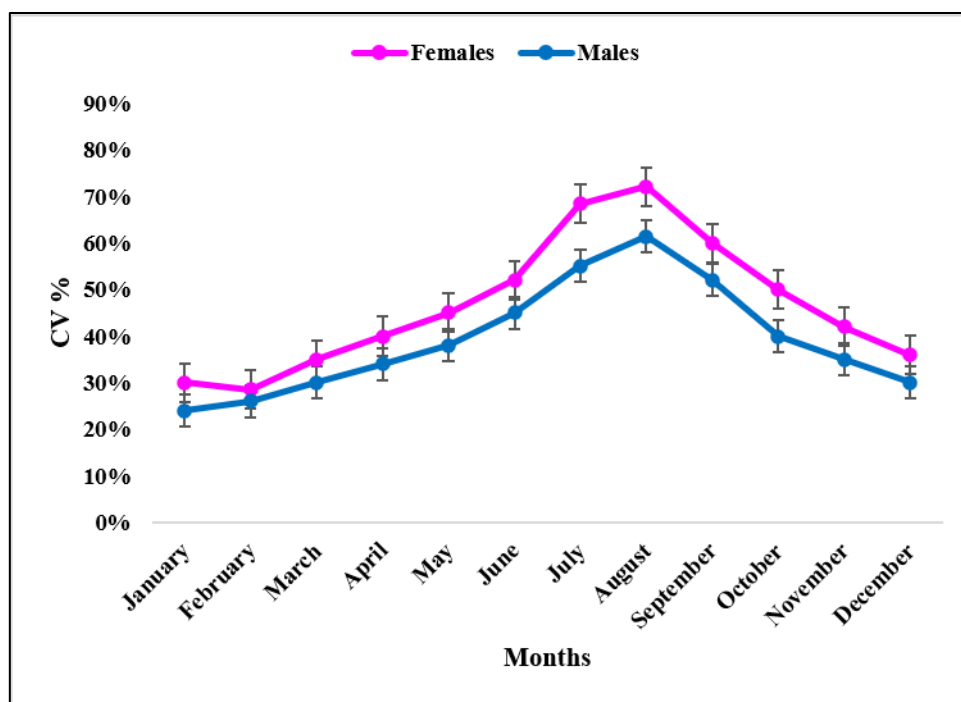


Fig. 4. Monthly variation of the vacuity coefficient (Cv%) according to Sex in *Solea solea* from Oran Bay.

Variation of the Vacuity Coefficient (Cv%) According to Size Classes

Stomachs of *Solea solea* were divided into two size classes based on total length: smaller individuals (TL < 20 cm) and larger individuals (TL ≥ 20 cm). The results showed that smaller individuals exhibited lower vacuity coefficient values (38.02%) compared to larger individuals (52.98%). Conversely, specimens with a total length equal to or greater than 20 cm presented higher Cv% values, indicating a greater proportion of empty stomachs (Fig. 5).

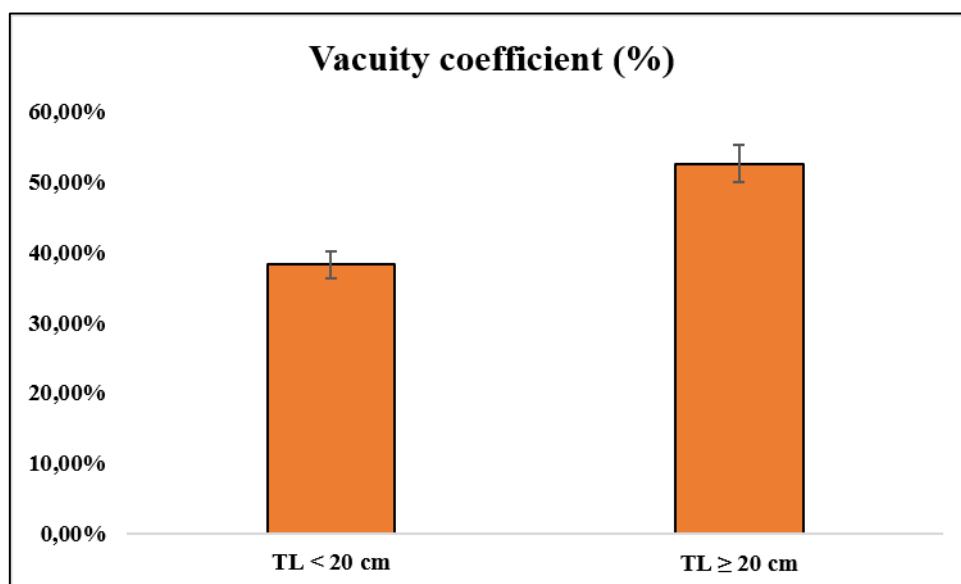


Fig. 5. Variation of the vacuity coefficient (Cv%) according to size classes in *Solea solea* from Oran Bay.

Variation of the Vacuity Coefficient (Cv%) and Gonadosomatic Index (GSI)

The relationship between monthly variations in the vacuity coefficient (Cv%) and the gonadosomatic index (GSI%) in female *Solea solea* was assessed using Pearson correlation analysis. GSI values were expressed as percentages. The analysis revealed a strong and significant negative correlation between Cv% and GSI% ($r = -0.953$, $df = 10$, $p < 0.001$, $R^2 = 0.908$; Table 4). The lowest Cv% values were observed in February (28.57%) and March (35.00%), when GSI reached its highest values of 6.40% and 6.10%, respectively. Conversely, Cv% increased during summer, reaching 68.42% in July and 72.15% in August, whereas GSI decreased to 2.40% and 1.90%, respectively (Fig. 6).

Table 4. Correlation analysis between monthly Cv% and GSI% in female *Solea solea* from Oran Bay.

Variables compared	n	Test	r	df	p-value	R ²
Cv% vs GSI%	12	Pearson correlation	-0.953	10	< 0.001	0.908

Note. n = number of months.

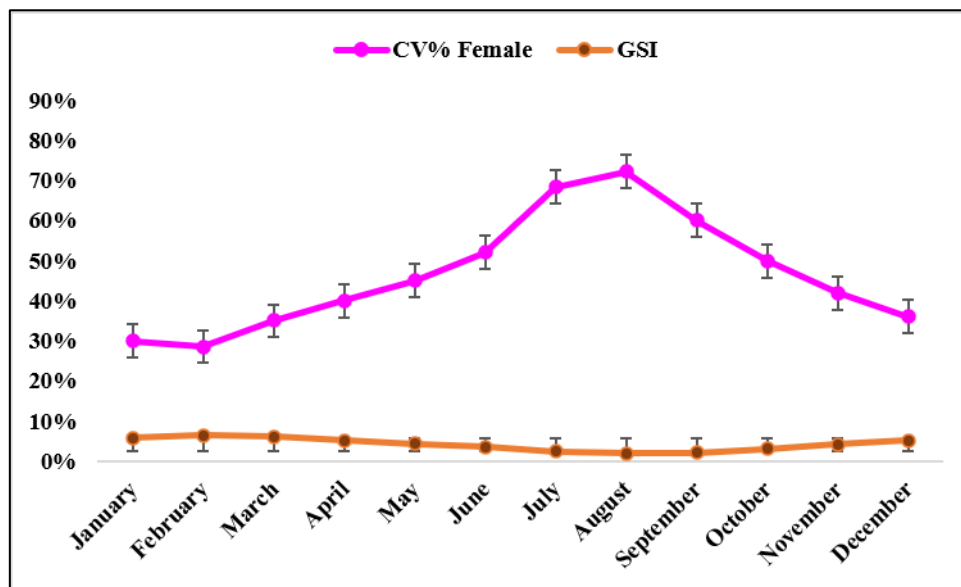


Fig. 6. Monthly variation of the vacuity coefficient (Cv%) and gonadosomatic index (GSI) in female *Solea solea* from Oran Bay.

Frequency of Occurrence (F%) of Prey Items in the Diet of *Solea solea*

The frequency of occurrence (F%) analysis of stomach contents in *Solea solea* revealed that crustaceans were the most frequently occurring prey category, being present in 89.39% of non-empty stomachs, indicating their dominant and consistent contribution to the diet. Polychaetes represented the second most important group, occurring in 65.15% of the examined stomachs. Bivalves were recorded in 31.82% of stomachs, followed by gastropods (19.70%). Unidentified prey items were observed in 12.63% of stomachs. Nematodes (8.59%) and ascidians (7.07%) showed the lowest occurrence frequencies, with ascidians representing the least frequent prey category (Fig. 7).

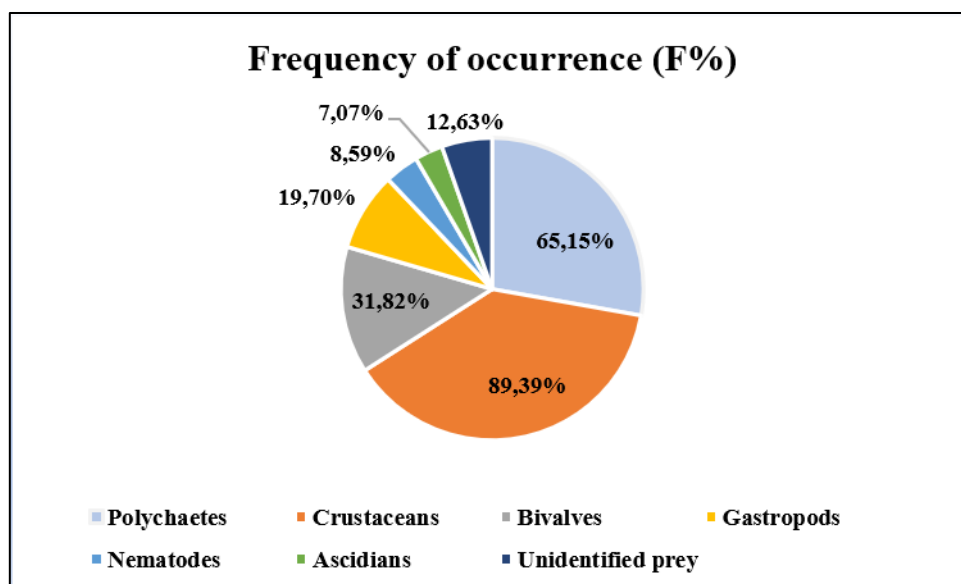


Fig.7. Frequency of occurrence (F%) of prey items in the diet of *Solea solea* from Oran Bay.

Seasonal Variation of Frequency of Occurrence (F%) of Prey Items in the Diet of *Solea solea*

Seasonal sample sizes and non-empty stomach counts, which served as denominators for the calculation of seasonal F% values, are presented in Table (5). Raw counts of each prey category by season are provided in Table (6).

The seasonal analysis of the frequency of occurrence (F%) of prey items in the diet of *Solea solea* from Oran Bay showed a clear dominance of crustaceans across all seasons. Their occurrence remained consistently high, reaching 88.46% in winter, 87.93% in spring, peaking at 95.12% in summer, and slightly decreasing to 87.23% in autumn, confirming their central role in the diet throughout the year. Polychaetes represented the second most important prey group, with relatively high but fluctuating values: 69.23% in winter, 65.52% in spring, a decrease in summer (58.54%), and a slight increase in autumn (65.96%). Bivalves showed moderate occurrence frequencies, varying from 36.54% in winter to 31.03% in spring, reaching a minimum in summer (24.39%) before increasing again in autumn (34.04%). Gastropods remained less frequent but exhibited a slight seasonal increase during summer (21.95%), compared to winter (19.23%), spring (18.97%), and autumn (19.15%). Nematodes and ascidians consistently showed low occurrence throughout the year. Nematodes varied from 7.69% in winter to 8.62% in spring, 9.76% in summer, and 8.51% in autumn. Ascidiens showed values of 7.69% in winter, 6.90% in spring, 7.32% in summer, and 6.38% in autumn. Unidentified prey items remained relatively stable, with values of 11.54% in winter, 13.79% in spring, 12.20% in summer, and 12.77% in autumn (Fig. 8).

Table 5. Seasonal sample sizes and vacuity coefficient (Cv%) of *Solea solea* from Oran Bay.

Season	Examined stomachs (n)	Empty stomachs (n)	Non-empty stomachs (n)	Denominator used for F% (n)	CV (%)	Non-empty (%)
Winter	74	22	52	52	29.73	70.27
Spring	93	35	58	58	37.63	62.37
Summer	103	62	41	41	60.19	39.81
Autumn	90	43	47	47	47.78	52.22
Total	360	162	198	198	45.00	55.00

Note. The number of non-empty stomachs per season (column "Non-empty stomachs, n") was used as the denominator for calculating the seasonal F% values reported above and in Fig. (8).

Table 6. Raw counts of prey categories by season (number of non-empty stomachs containing each prey category / total non-empty stomachs), used to calculate seasonal frequency of occurrence (F%) in the diet of *Solea solea* from Oran Bay.

Prey category	Winter n/N	Spring n/N	Summer n/N	Autumn n/N	Total n/N
Polychaetes	36/52	38/58	24/41	31/47	129/198
Crustaceans	46/52	51/58	39/41	41/47	177/198
Bivalves	19/52	18/58	10/41	16/47	63/198
Gastropods	10/52	11/58	9/41	9/47	39/198
Nematodes	4/52	5/58	4/41	4/47	17/198
Ascidians	4/52	4/58	3/41	3/47	14/198
Unidentified prey	6/52	8/58	5/41	6/47	25/198

Note. n = number of non-empty stomachs in which the prey category was recorded; N = total number of non-empty stomachs for that season.

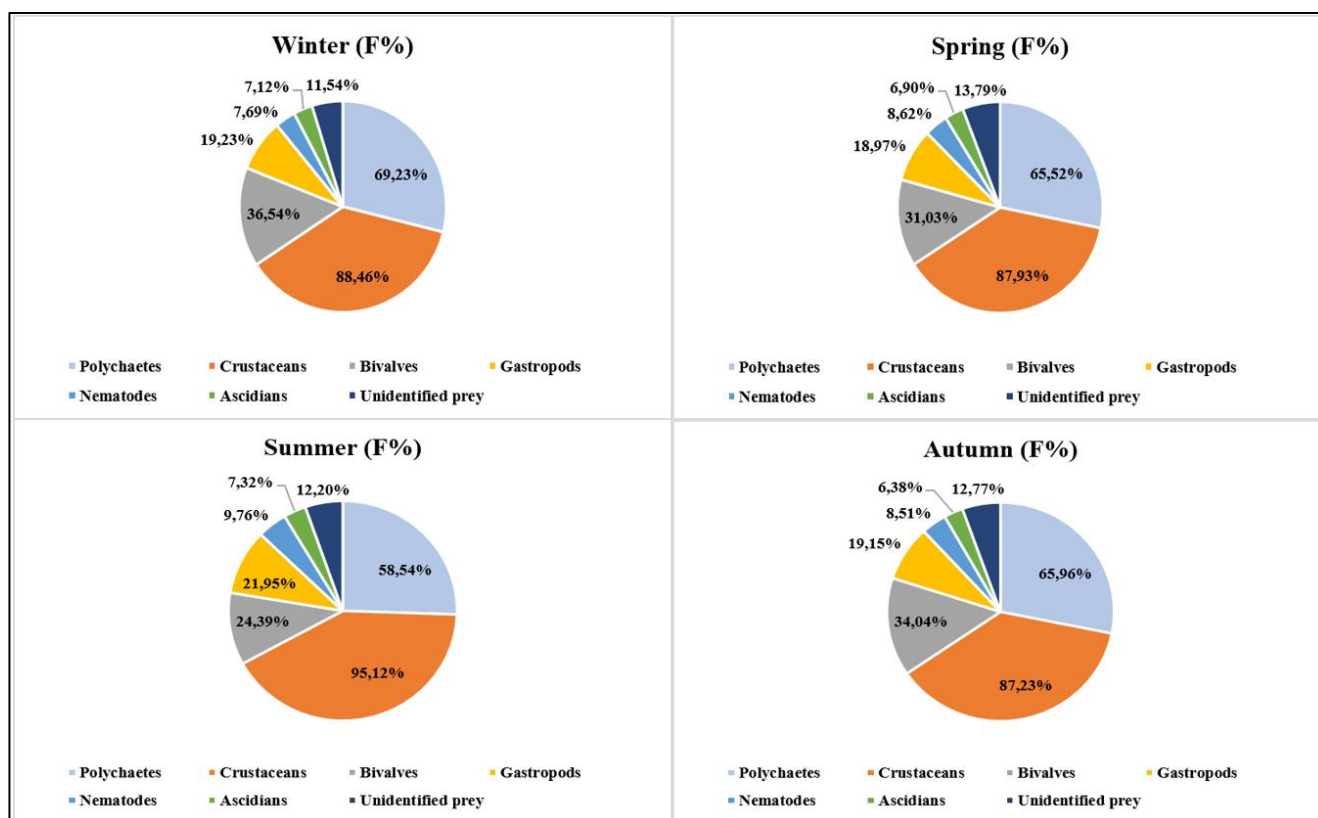


Fig. 8. Seasonal variation of frequency of occurrence (F%) of prey items in the diet of *Solea solea* from Oran Bay.

Numerical Percentage (Cn%) of Prey Items in the Diet of *Solea solea*

The numerical analysis (Cn%) of stomach contents in *Solea solea* revealed a total of 512 prey items distributed among several groups of benthic invertebrates. Crustaceans constituted the dominant prey category, with 206 items, representing 40.23% of the total ingested prey, followed by polychaetes with 169 items (33.01%). Bivalves accounted for 72 items (14.06%), while gastropods represented 30 items (5.86%). In contrast, nematodes (14 items; 2.73%) and ascidians (9 items; 1.76%) were the least represented prey categories in terms of numerical abundance, while unidentified prey comprised 12 items (2.34%) (Fig. 9).

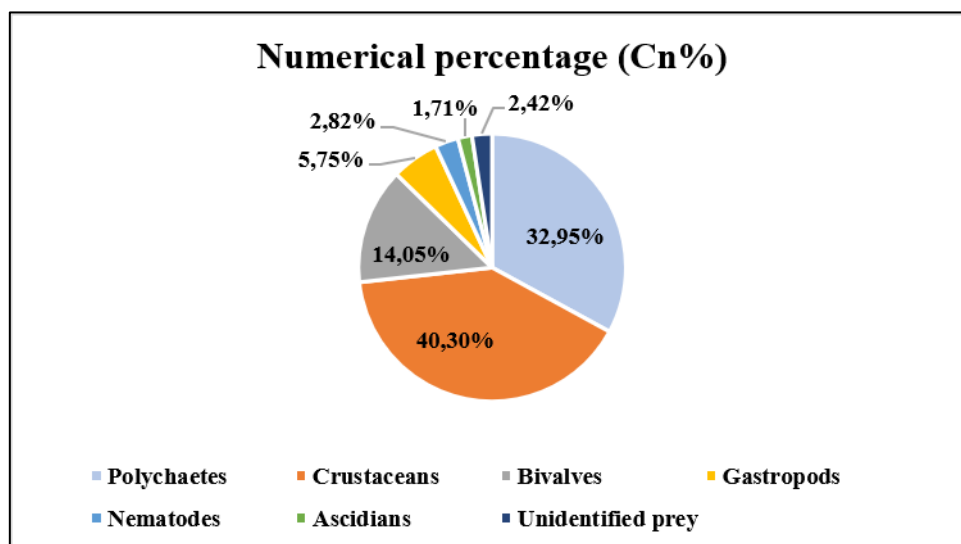


Fig. 9. Numerical percentage (Cn%) of prey items in the diet of *Solea solea* from Oran Bay.

Seasonal Variation in Numerical Diet Composition (Cn%) of *Solea solea*

The diet composition of *Solea solea* in Oran Bay showed descriptive seasonal variations based on the numerical percentage (Cn%) of prey items. In winter, polychaetes dominated with 51 items (36.69%), followed by crustaceans with 48 items (34.53%) and bivalves with 24 items (17.27%), while gastropods accounted for 7 items (5.04%). In spring, crustaceans became the dominant prey category, with 60 items (39.22%), followed by polychaetes with 53 items (34.64%) and bivalves with 23 items (15.03%). During summer, crustaceans reached their highest numerical contribution, with 62 items (48.06%), followed by polychaetes with 36 items (27.91%), bivalves with 11 items (8.53%), and gastropods with 10 items (7.75%). In autumn, crustaceans remained dominant with 36 items (39.56%), followed by polychaetes with 29 items (31.87%) and bivalves with 14 items (15.38%), while gastropods accounted for 6 items (6.59%). Nematodes, ascidians, and unidentified prey remained numerically low across all seasons (Fig. 10 & Table 7).

To evaluate whether these seasonal differences in diet composition were statistically significant, a contingency analysis was performed using prey counts by season and prey category. The Pearson chi-square test did not reveal a significant seasonal difference in numerical diet composition ($\chi^2 = 12.15$, $df = 18$, $p = 0.840$). Similarly, the likelihood-ratio G-test produced a non-significant result ($G = 12.61$, $df = 18$, $p = 0.814$; Table 8). Although the low expected frequencies for some rare prey categories (nematodes, ascidians, unidentified prey) may affect the reliability of the chi-square approximation, the convergence of results between both tests supports the conclusion that seasonal differences in diet composition were not statistically.

Table 7. Numerical composition (raw counts and Cn%) of prey items by season in the diet of *Solea solea* from Oran Bay.

Prey category	Winter n (%)	Spring n (%)	Summer n (%)	Autumn n (%)	Total n (%)
Polychaetes	51 (36.69)	53 (34.64)	36 (27.91)	29 (31.87)	169 (33.01)
Crustaceans	48 (34.53)	60 (39.22)	62 (48.06)	36 (39.56)	206 (40.23)
Bivalves	24 (17.27)	23 (15.03)	11 (8.53)	14 (15.38)	72 (14.06)
Gastropods	7 (5.04)	7 (4.58)	10 (7.75)	6 (6.59)	30 (5.86)
Nematodes	3 (2.16)	4 (2.61)	4 (3.10)	3 (3.30)	14 (2.73)
Ascidians	2 (1.44)	2 (1.31)	3 (2.33)	2 (2.20)	9 (1.76)
Unidentified	4 (2.88)	4 (2.61)	3 (2.33)	1 (1.10)	12 (2.34)
Total	139 (100)	153 (100)	129 (100)	91 (100)	512 (100)

Note. n = number of prey items recorded for each category; percentages in parentheses represent the numerical percentage (Cn%) relative to the seasonal or annual total.

Table 8. Statistical comparison of seasonal diet composition in *Solea solea* from Oran Bay.

Test	Statistic	df	p-value	Interpretation
Pearson chi-square	$\chi^2 = 12.15$	18	0.840	Not significant
Likelihood-ratio G-test	$G = 12.61$	18	0.814	Not significant

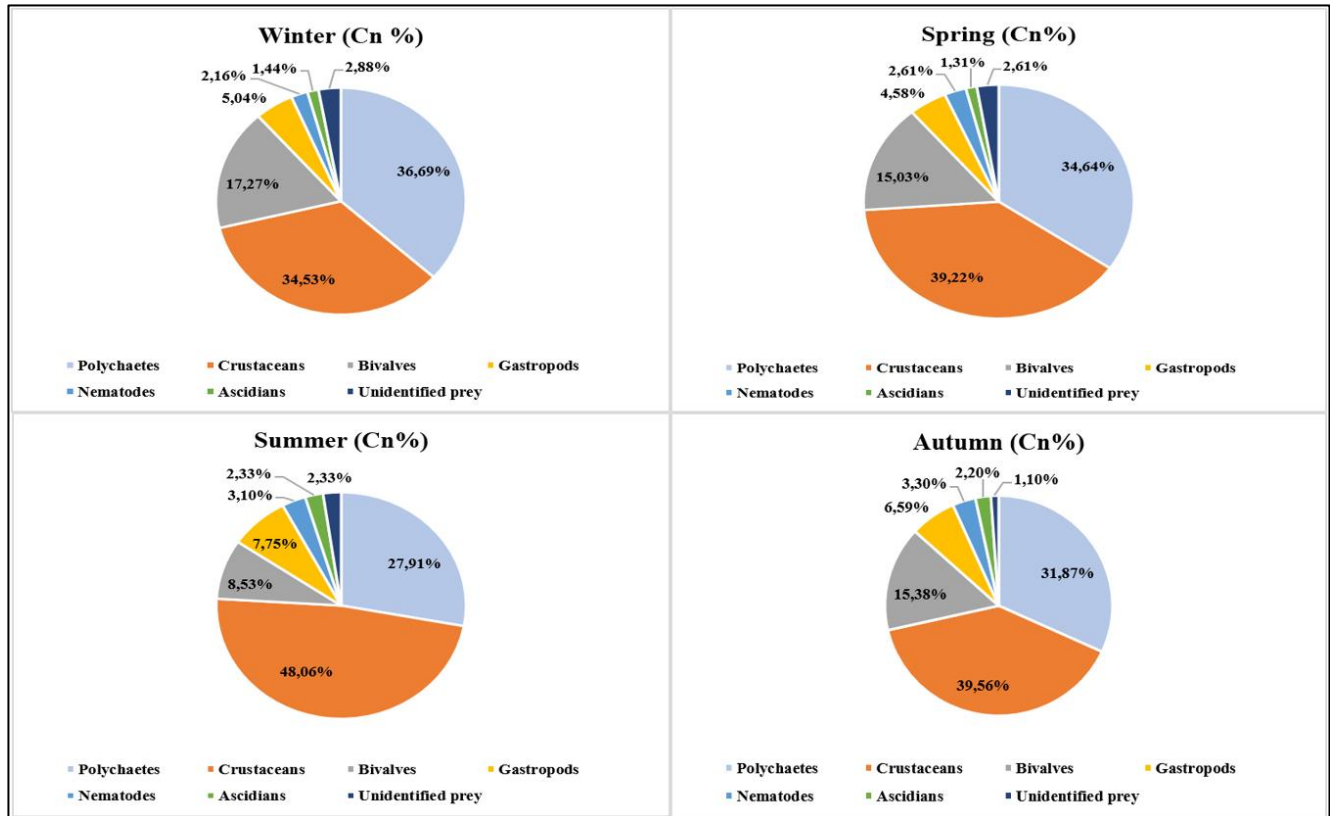


Fig. 10. Seasonal variation of numerical percentage (Cn%) of prey items in the diet of *Solea solea* from Oran Bay.

Variation of the Diet According to Size Classes

Frequency of Occurrence (F%) According to Size Classes

Sample sizes and non-empty stomach count for each size class are presented in Table (9). Raw counts of each prey category by size class are provided in Table (10). The analysis of the frequency of occurrence (F%) of prey items according to size classes revealed notable differences in the diet of *Solea solea* from Oran Bay. In smaller individuals (TL < 20 cm), crustaceans represented the most frequently occurring prey category (85.71%), followed by polychaetes (72.27%), bivalves (25.21%), and gastropods (14.29%). Nematodes (11.76%) and ascidians (10.08%) showed relatively higher occurrence frequencies in this size class compared to larger individuals, while unidentified prey items were recorded in 10.92% of stomachs (Fig. 11). In larger individuals (TL ≥ 20 cm), crustaceans were also the most frequently consumed prey group (94.94%), followed by polychaetes (54.43%), bivalves (41.77%), and gastropods (27.85%). Nematodes (3.80%) and ascidians (2.53%) showed markedly lower occurrence frequencies in this size class, whereas unidentified prey items showed a higher occurrence (15.19%) compared to smaller individuals (Fig. 11).

Table 9. Sample sizes and vacuity coefficient (Cv%) by size class of *Solea solea* from Oran Bay.

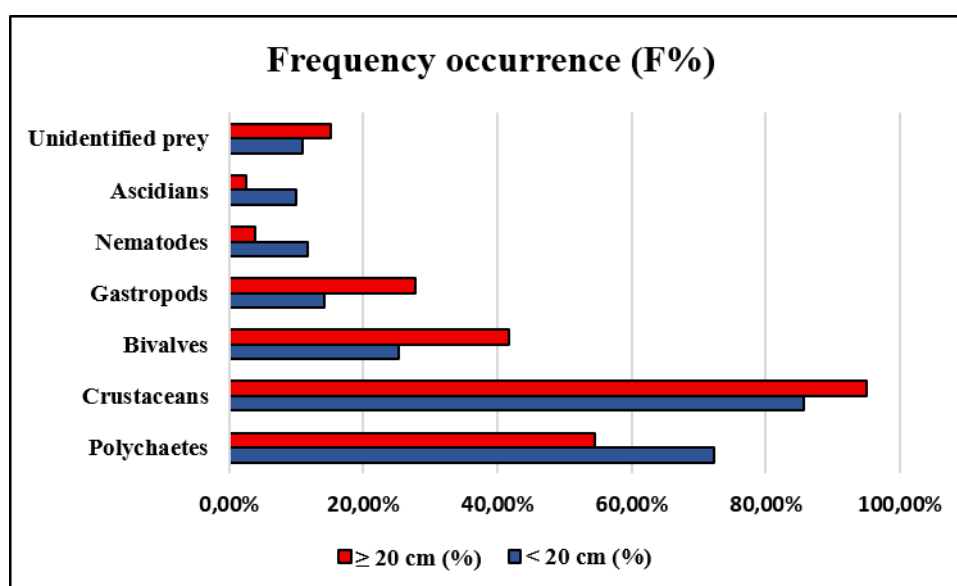
Size class	Examined fish/stomachs (n)	Empty stomachs (n)	Non-empty stomachs (n)	Cv (%)	Non-empty (%)
TL < 20 cm	192	73	119	38.02	61.98
TL ≥ 20 cm	168	89	79	52.98	47.02
Total	360	162	198	45.00	55.00

Note. n = number of individuals (stomachs) per size class.

Table 10. Raw counts of prey categories by size class, used to calculate F%.

Prey category	TL < 20 cm (n/N)	F (%)	TL ≥ 20 cm (n/N)	F (%)
Polychaetes	86/119	72.27	43/79	54.43
Crustaceans	102/119	85.71	75/79	94.94
Bivalves	30/119	25.21	33/79	41.77
Gastropods	17/119	14.29	22/79	27.85
Nematodes	14/119	11.76	3/79	3.80
Ascidians	12/119	10.08	2/79	2.53
Unidentified prey	13/119	10.92	12/79	15.19

Note. n = number of non-empty stomachs in which the prey category was recorded; N = total number of non-empty stomachs for that size class.

**Fig. 11.** Frequency of occurrence (F%) of prey items according to size classes in *Solea solea* from Oran Bay.

Numerical Percentage (Cn%) According to Size Classes

The numerical percentage (Cn%) analysis further characterized dietary differences between size classes. In smaller individuals (TL < 20 cm), polychaetes constituted the dominant prey category (39.20%), followed by crustaceans (33.80%), bivalves (12.10%), nematodes (4.50%), gastropods (3.80%), unidentified prey (3.50%), and ascidians (3.10%) (Fig. 12). In larger individuals (TL ≥ 20 cm), crustaceans became the numerically dominant prey group (48.60%), followed by polychaetes (25.10%), bivalves (16.60%), and gastropods (8.20%). Nematodes (0.80%), unidentified prey (0.60%), and ascidians (0.10%) were poorly represented in this size class (Fig. 12).

Trophic niche breadth, estimated using Levin's standardized index (Bsta; **Levins, 1968**) based on Cn% proportions, was higher in smaller individuals (Bsta = 0.412) than in larger individuals (Bsta = 0.333), consistent with the Shannon diversity index (**Shannon, 1948**; $H' = 1.478$ vs. 1.277, respectively; Table 11). These results indicate that smaller individuals exploit a comparatively broader range of prey categories, whereas larger individuals show a more specialized diet increasingly focused on crustaceans.

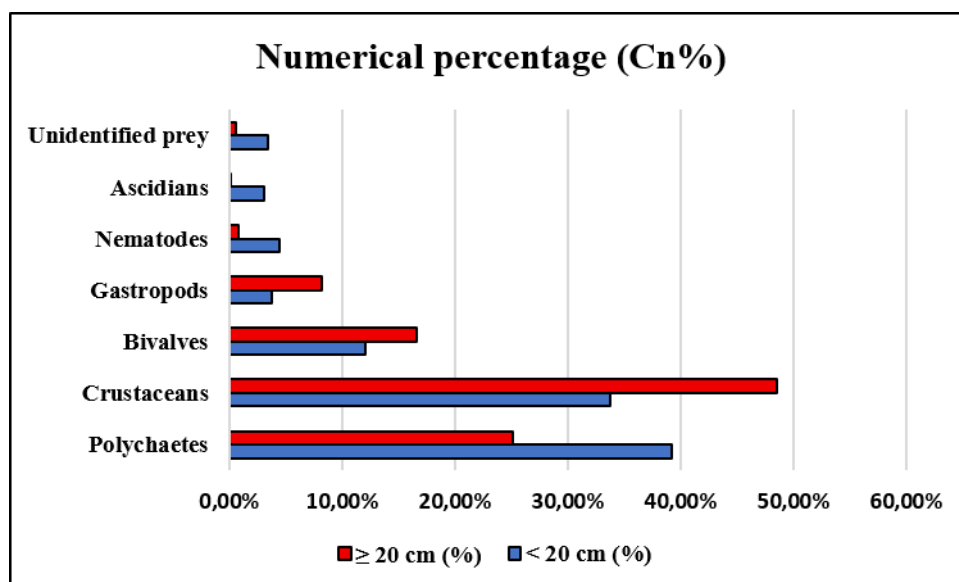


Fig. 12. Numerical percentage (Cn%) of prey items according to size classes in *Solea solea* from Oran Bay.

Table 11. Trophic niche breadth indices by size class in *Solea solea* from Oran Bay.

Size class	Levin's standardized index (Bsta)	Shannon diversity index (H')
TL < 20 cm	0.412	1.478
TL ≥ 20 cm	0.333	1.277

Note. Bsta = Levin's standardized niche breadth index (Levins, 1968), ranging from 0 (specialist diet) to 1 (generalist diet); H' = Shannon diversity index (Shannon, 1948), calculated from Cn% proportions of each prey category.

Feeding Indices and Prey Classification

The values of the calculated feeding indices (Q, IA, and IRI) show marked differences among prey categories (Table 9). These indices classify prey into categories according to specific thresholds:

Hureau's coefficient ($Q = Cn\% \times Cp\%$) distinguishes preferential prey ($Q > 200$), secondary prey ($20 < Q < 200$), and accessory prey ($Q < 20$) (Table 13); Lauzanne's alimentary index ($IA = F\% \times Cp\%/100$) distinguishes dominant prey ($IA > 50$), essential prey ($25 < IA \leq 50$), non-negligible prey ($10 < IA \leq 25$), and secondary prey ($IA \leq 10$) (Table 14); and the index of relative importance ($IRI = F\% \times (Cn\% + Cp\%)$) distinguishes principal prey ($200 < IRI < 20000$), secondary prey ($20 < IRI < 200$), and accidental prey ($IRI < 20$) (Table 15).

Crustaceans exhibited the highest values for all three indices, followed by polychaetes. Bivalves displayed intermediate values, whereas gastropods, nematodes, ascidians, and unidentified prey showed lower values for all indices. These discrepancies between indices arise from their different mathematical structures: Q relies solely on numerical and weight contributions ($Cn\% \times Cp\%$), IRI additionally incorporates frequency of occurrence ($F\%$), and IA weights biomass by frequency rather than abundance. As a result, prey categories that are frequently encountered but numerically scarce, such as bivalves and gastropods, may receive different rankings depending on the index used, illustrating the complementary nature of these indices in characterizing dietary importance.

Table 9. Values of different feeding indices in *Solea solea* from Oran Bay.

Prey Category	Cn (%)	Cp (%)	F (%)	Q	IA	IRI
Polychaetes	32.95	28.40	65.15	935.78	18.50	3996.95
Crustaceans	40.30	45.20	89.39	1821.56	40.40	7624.85
Bivalves	14.05	13.80	31.82	193.89	4.39	886.19
Gastropods	5.75	6.90	19.70	39.68	1.36	249.21
Nematodes	2.82	1.50	8.59	4.23	0.13	37.11
Ascidians	1.71	1.20	7.07	2.05	0.08	20.57
Unidentified prey	2.42	3.00	12.63	7.26	0.38	68.45

The values of Q (Hureau, 1970) and IRI (Pinkas *et al.*, 1971) show that crustaceans and polychaetes are essential prey items, being classified as dominant prey according to Q (Table 13) and as principal prey according to IRI (Table 15), reflecting their relative importance in the observed diet rather than true prey preference, which would require independent data on prey availability in the environment. In contrast, the IA (Lauzanne, 1975) indicates that crustaceans are essential prey, while polychaetes are classified as non-negligible prey (Table 14).

Bivalves are considered secondary prey according to the Q index (Table 13), and principal prey according to the IRI index (Table 15). This contradiction arises from the different mathematical structure of the two indices: Q is based solely on numerical and weight contributions ($Cn\% \times Cp\%$), whereas IRI additionally incorporates frequency of occurrence ($F\%$); bivalves, despite moderate numerical and weight values, occurred frequently enough ($F\% = 31.82\%$) to be ranked as principal prey under IRI . Nematodes and ascidians were consistently classified as low-importance prey, being ranked as accessory prey according to Q and secondary prey according to IRI (Tables 13, 15).

Table 13. Classification of prey ingested by *Solea solea* from Oran Bay according to the method of Hureau (1970).

Classification	Type of prey
Q > 200 (dominant prey)	Crustaceans, Polychaetes
20 < Q < 200 (secondary prey)	Bivalves, Gastropods
Q < 20 (accessory prey)	Nematodes, Ascidians, Unidentified prey

Table 14. Classification of prey ingested by *Solea solea* from Oran Bay according to the method of Lauzanne (1975).

Classification	Type of prey
IA ≤ 10 (secondary prey)	Bivalves, Gastropods, Nematodes, Ascidians, Unidentified prey
10 < IA ≤ 25 (non-negligible prey)	Polychaetes
25 < IA ≤ 50 (essential prey)	Crustaceans
IA > 50 (dominant prey)	/

Table 15. Classification of prey ingested by *Solea solea* from Oran Bay according to the method of Pinkas *et al.* (1971).

Classification	Type of prey
200 < IRI < 20000 (principal prey)	Crustaceans, Polychaetes, Bivalves, Gastropods
20 < IRI < 200 (secondary prey)	Nematodes, Ascidians, Unidentified prey
IRI < 20 (accidental prey)	/

DISCUSSION

The overall vacuity coefficient (45%) is consistent with the low daily food consumption and intermittent feeding pattern typically reported in common sole (Cabral, 2000; Vinagre & Cabral, 2008). Part of this high vacuity may also reflect methodological factors rather than feeding biology alone: stomach evacuation or regurgitation can occur during trawling and net retrieval, and the time elapsed between capture and dissection may have allowed further digestion of stomach contents, both of which are known to inflate apparent vacuity in trawl-caught benthic fish (Bowman, 1986; Amundsen & Sánchez-Hernández, 2019). Although females showed a numerically higher Cv% (48.57%) than males (40%), this difference was not statistically significant ($\chi^2 = 2.60$, $df = 1$, $p = 0.107$; Table 3), indicating no clear sex-based difference in feeding intensity in this population. Monthly variations nonetheless revealed a consistent seasonal pattern in both sexes, with minimal vacuity in winter and maximal vacuity in summer (Fig. 4).

This seasonal pattern was strongly linked to the reproductive cycle in females: a significant negative Pearson correlation was found between monthly Cv% and GSI% ($r = -0.953$, $df = 10$, $p < 0.001$; Table 4), with feeding activity peaking during gonadal maturation (February-March) and declining sharply after spawning (July-August). This is consistent with Carrozzi *et al.* (2022) in the central Adriatic Sea and with Tabeche (2022), who reported a similar reproductive timing and a higher gonadosomatic investment in females for the same Oran Bay population (Fanelli *et al.*, 2022).

Smaller individuals (TL < 20 cm) showed lower Cv% (38.02%) than larger individuals (52.98%), consistent with the higher metabolic demands of somatic growth in juveniles (Sánchez-Hernández *et al.*, 2022). The higher vacuity in larger individuals may partly reflect reproductive investment,

although this interpretation remains tentative, as maturity stage and sex distribution were not assessed independently within each size class; larger individuals likely include both sexes and a range of reproductive states, and the observed pattern should therefore be regarded as descriptive rather than conclusive evidence of a reproduction-driven mechanism.

The diet of *Solea solea* in Oran Bay comprised a diverse assemblage of benthic invertebrates (512 prey items across several taxonomic groups, including the annelid class Polychaeta, crustaceans, molluscs, nematodes, and ascidians), dominated by crustaceans (F% = 89.39%; Cn% = 40.30%; Table 9) and polychaetes (F% = 65.15%; Cn% = 32.95%; Table 9), consistent with the benthophagous, opportunistic strategy reported elsewhere for this species (Cabral, 2000; Teixeira & Cabral, 2010; Carrozzi *et al.*, 2022; Fanelli *et al.*, 2022). This crustacean dominance likely reflects their high local abundance and availability on sandy-muddy substrates, combined with their relatively low mobility and small size, which make them readily accessible to the small, ventrally oriented mouth typical of *Solea solea* and other soft-bottom flatfish (de Groot, 1971). Feeding indices (Q, IRI) confirmed crustaceans and polychaetes as dominant/principal prey, while bivalves and gastropods, despite moderate abundance, ranked as principal prey under IRI due to their high frequency of occurrence; the IRI-based classification was retained as the primary reference, as it integrates frequency, abundance, and biomass (Pinkas *et al.*, 1971; Cortés, 1997). These rankings reflect dietary importance rather than true prey preference, which would require independent data on prey availability in the environment (Amundsen *et al.*, 1996).

Studies on Mediterranean soles have similarly shown that benthic prey, particularly polychaetes, molluscs and crustaceans, are central components of sole diets, supporting the interpretation of a benthic feeding pattern in the present samples (Sharaf *et al.*, 2007).

Seasonal differences in diet composition were observed descriptively (e.g., crustacean occurrence peaking in summer at 95.12%; Fig. 8), but a contingency analysis found no statistically significant seasonal variation in numerical diet composition ($\chi^2 = 12.15$, $G = 12.61$, $df = 18$, $p > 0.05$; Table 8). As benthic invertebrate availability in Oran Bay was not independently measured, these seasonal trends cannot be directly attributed to changes in prey abundance in the environment, and the underlying mechanisms remain inferred rather than demonstrated; they are nonetheless consistent with the generally opportunistic feeding behavior reported for this species (Carrozzi *et al.*, 2022; Fanelli *et al.*, 2022).

A descriptive ontogenetic shift was observed between size classes, smaller individuals showing a broader trophic niche (Levin's Bsta = 0.412; Shannon H' = 1.478; Table 11) than larger individuals (Bsta = 0.333; H' = 1.277; Table 11), which fed more heavily on crustaceans. As size classes were defined using a total-length threshold (20 cm) rather than direct maturity staging, this pattern should be interpreted as a size-related trend rather than a confirmed maturity-linked shift; it is nonetheless consistent with the general expectation that ontogenetic diet shifts reduce intraspecific competition and allow access to larger, more energetically profitable prey with growth (Amara *et al.*, 2001; Sánchez-Hernández *et al.*, 2022), a pattern also reported for this species elsewhere in the Mediterranean and Atlantic (Cabral, 2000; Teixeira & Cabral, 2010; Carrozzi *et al.*, 2022; Fanelli *et al.*, 2022).

CONCLUSION

The present study provides a concise assessment of the feeding ecology of *Solea solea* in Oran Bay based on stomach content analysis of 360 individuals. The results suggest an opportunistic and flexible benthophagous feeding strategy, dominated by benthic invertebrates such as crustaceans, polychaetes, bivalves, gastropods, nematodes, and ascidians. The overall vacuity coefficient of 45% may reflect alternating periods of high and reduced feeding activity, while remaining limited to evidence derived from stomach contents.

The F%, Cn%, Cp%, Q, IA, and IRI indices identified crustaceans and polychaetes as the most important dietary components. Bivalves occupied an intermediate position, whereas gastropods, nematodes, ascidians, and unidentified prey showed lower importance. These results indicate the relative importance of prey in the observed diet but do not demonstrate true prey preference, because prey availability in the environment was not measured.

Seasonal variations were observed descriptively, with crustaceans dominating throughout the year and polychaetes contributing more during the cold season. However, in the absence of independent measurements of prey availability, benthic macrofauna, stable isotopes, and environmental drivers, these variations cannot be conclusively attributed to prey selection or environmental changes.

The inverse relationship between the vacuity coefficient and the gonadosomatic index suggests a possible energetic trade-off between feeding and reproduction in females. Similarly, the differences observed between size classes suggest a size-related dietary shift, with smaller individuals showing a polychaete-rich diet and larger individuals showing a diet more centered on crustaceans. These interpretations should remain cautious because they are not based on direct maturity measurements or additional experimental data.

Overall, this study provides useful baseline data on the trophic ecology of *Solea solea* along the western Algerian coast. The results support its role as a benthic predator in coastal food webs and highlight the need for continued monitoring. Future studies should integrate stable isotope analysis, prey availability assessment, benthic macrofauna sampling, and environmental data to better distinguish dietary importance from true prey preference.

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