Journal of
*Marine Science and Engineering*

*Review*

# Overview of Predation by Birds, Cephalopods, Fish and Marine Mammals on Marine Benthic Amphipods

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**Abstract:** With about 8000 marine benthic species, the amphipod crustaceans form one of the richest animal groups of the worldwide Ocean. They have colonized a wide range of soft- and hard-bottom natural and artificial habitats extending from the intertidal to hadal zones. Moreover, they show a broad size spectrum, with numerous giant species exceeding 20 cm in length and some species smaller than 2 mm. When biofouling artificial hard surfaces, some tube-building species can form very dense populations comprising up to 100,000 individuals per square meter. Amphipods are important prey for fish and mammals. Along with cephalopod juveniles, they are also included in the trophic diet of shorebirds that consume amphipods mostly during the low tide on tidal flats. They display diel migration, which reinforces the predation by demersal fish in the suprabenthic zone just above the sea bed, as well as by pelagic fish in the water column. Despite their importance in terms of biodiversity and trophic transfer, no general overview is available on the role of benthic amphipods in marine ecosystem food webs. Various methods, including laboratory and field experiments, as well as the analysis of stomach contents and DNA extraction, have been used to identify the prey/predator trophic links. Based on an extensive literature review, this study discusses the role of marine benthic amphipods as potential food for higher trophic levels in natural and artificial hard-bottom communities created via the construction of offshore wind farms.

**Keywords:** amphipod; predation; predator; prey; fish; bird; cephalopod; mammals

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**Citation:** Dauvin, J.-C. Overview of Predation by Birds, Cephalopods, Fish and Marine Mammals on Marine Benthic Amphipods. *J. Mar. Sci. Eng.* **2024**, *12*, 403. https://doi.org/10.3390/jmse12030403

Academic Editor: Sílvia C. Gonçalves

Received: 29 January 2024
Revised: 22 February 2024
Accepted: 23 February 2024
Published: 26 February 2024

## 1. Introduction

The total number of marine, brackish, freshwater and terrestrial species of amphipods exceeds 10,000 [1]. Among them, about 8000 are marine benthic species, while the number of marine pelagic species is lower and accounts for about 300 species. These pelagic species show a very wide geographical distribution, while the benthic amphipods show a high proportion of endemic species with limited spatial distribution. In sub-Antarctic waters, amphipod pelagic species such as *Themisto gaudichaudii* Guérin, 1825, and *Primno macropa* Guérin-Méneville, 1836, form very large swarms, are considered major trophic sources and are the second group of animal prey after euphausiids [2]. In the same way, all the seabird families in the Antarctic and Sub-Antarctic have been reported to feed on pelagic amphipods [2]. Birds feed on amphipods, but in the Sub-Antarctic, only in procellariids was amphipod prey deemed important (>10% by number and/or reconstituted mass) in the diet. In penguins and cormorants, it was secondary (regularly present but <10%), and it was rare in albatrosses [2].

Benthic amphipods are distributed from the supralittoral to the hadal zones, but most of them live on the continental shelf from 0 to 200 m in depth [3]. They are keystone organisms, often representing the dominant component among benthic macroinvertebrates along with the polychaetes and the mollusks, playing a crucial role in marine food webs, in which they act as secondary producers and food sources for various predators [4,5]. It is known that amphipods represent an important source of food for many organisms at different trophic levels on the sea bottom, as well as in the suprabenthic layer and the water column [6–8]. As with other peracarid species, amphipods participate in an important bentho-pelagic flux of energy throughout the Benthic Boundary Layer [9]. Moreover, they are important contributors to marine productivity [10]. Amphipods are consumed by some infaunal species, such as carnivorous polychaetes and nemerteans (see, for example, [11,12]). Ref. [13] has also shown that the Asian shore crab—the non-indigenous species (NIS) *Hemigrapsus sanguineus* (De Haan, 1835)—feeds on the NIS amphipod *Ptilohyale littoralis* (Stimpson, 1853), which confirms the preliminary experiments of [14] on the consumption of amphipods by the invasive species *H. sanguineus*. Conversely, some amphipods are known to be predators or necrophagous species such as numerous Lysianassoids, which range from shallow to deep waters. Other families, such as the Phoxocephalidae, predate on larvae and juveniles in marine soft-bottom communities [11]. Dense populations of the ampeliscid amphipod *Haploops nirae* Kaïm-Malka, 1976, act as an engineer species in the shallow waters (15–35 m) of Concarneau Bay on the northern coast of the Bay of Biscay, France [15].

Nevertheless, in spite of the development of studies of macrobenthos as a branch of fisheries research, there is still very little work on the functional relationships between benthic prey populations and demersal fish [16–18]. Several studies have been carried out on the importance of amphipods in the diets of demersal fish, mainly in the Northeast Atlantic (for example [19–23]). Amphipods are found to be largely consumed by demersal fish, regularly as principal and accessory prey, while certain benthic amphipods are over-represented in the stomach contents of fish showing a preferential source of food [18]. Recent reviews of our knowledge of marine biodiversity in the Southern Ocean have highlighted the importance of pelagic and benthic amphipods in this polar environment and their major role in the trophodynamics of Antarctic ecosystems, both as consumers and as prey [3,4,24,25]. Ref. [24] found a total of 176 amphipod species in the stomach contents of bird, fish and mammal top predators. The amphipod families showing the highest occurrence in stomach contents are the Lysianassoidea, Eusiridae and Epimeriidae in the case of the gammarids and the Hyperiidae and Vibiliidae in the case of the hyperiids. These latter authors [24] also stress that some families, like the Iphimediidae, are not commonly found in top predator stomachs, even though these families are well represented in the Antarctic Ocean. This is probably because of their particular spinose morphology, which should protect them from heavy predation.

Similarly, abundant literature exists on the relationship between the gray whale *Eschrichtius robustus* (Lilljeborg, 1861) and the dense Ampeliscidae amphipod populations along the North American Pacific coast and in the Arctic Ocean [26,27].

As regards birds, abundant literature is available on the role of the dense Corophiid populations, mainly concerning *Corophium volutator* (Pallas, 1766), in the food web of shorebirds, while amphipods often represent accessory prey for numerous other marine birds, mainly in the Southern Ocean and polar areas [2]. Finally, amphipods are consumed by some cephalopods living near the sea bed, and they have been proposed as a major food for cephalopod culture during their first stage of life.

The main aim of this present overview is to summarize the available information about benthic amphipods as prey for birds, cephalopods, fish and mammals. Based on extensive literature, I discuss the importance of marine benthic amphipods as potential food for higher trophic levels in natural communities and artificial hard-bottom communities that are created via the construction of offshore wind farms. Appendix A presents a synthesis of the relationship between predators and their amphipod prey cited in this review.

## 2. Methods of Analysis

### 2.1. Direct Observations

The diet of the guillemots *Uria aalge* (Pontoppidan, 1763) and *U. Zomvia* (Linnaeus, 1758) in the Barents Sea region has been studied during the summer breeding season mostly via direct observation of food items brought to the chick by the adults [28]. Controls were carried out by catching fish-carrying birds with a noose pole and identifying the food item by hand.

### 2.2. Stomach Contents

Stomach content analysis is a classical approach used to investigate short-term feeding ecology, as it provides a snapshot of recently ingested food items. It allows prey determination at the species level, using hard parts that resist digestion, such as crustacean exoskeletons, cephalopod beaks, fish otoliths and bones. However, one major limitation of this approach is the digestion of prey material, which can limit the identification of the prey and, thus, introduce biases towards certain taxonomic groups. Another bias can be due to the fact that amphipods may be ingested as prey items included in the guts of prey, and evidence of amphipod presence (whether physical, DNA or stable isotopes) may be secondary/incidental. Stomach content analysis has been widely used for fish for more than a century, and it remains a good method to examine feeding ecology (see, for example, [13,16,18,19,21,29,30]). It has also been applied to cuttlefish such as *Sepia officinalis* (Linnaeus, 1758) [31–33]. While stomach content analysis is a low-cost method that is still very widely used today, it nevertheless requires a very good knowledge of invertebrate fauna, including amphipods, to identify the food items and reduce determination times.

### 2.3. Fecal Samples

To identify the diet of the Turnstone *Arenaria interpres* Linnaeus, 1758, [34] studied the pellets deposited by this shorebird on beaches in North Wales (United Kingdom). Similarly, ref. [35] collected fresh fecal samples to identify the prey of the Westland petrel *Procellaria westlandica* Falla, 1946, a species endemic to the South Island of New Zealand. Ref. [36] examined the potential consumption of amphipods by shorebirds during their spring migration through Delaware Bay via the amplification of prey DNA fragments in feces using amphipod-specific primers. Refs. [37,38] determined the prey species of the gray whale via an analysis of fecal samples.

### 2.4. Stable Isotopes

Since prey is often difficult to identify in relation to its digestion within the stomach contents, an alternative approach is to use stable isotopes as indirect tracers of diet composition. Stable isotope analysis is a robust and commonly used tool in ecological studies to investigate trophic relationships and the trophic web structure integrated across time and space, providing long-term information on species' feeding ecology [33,39,40]. This approach is based on predictable differences between the isotopic signature of a consumer and its prey. Nitrogen isotope ratios are used to identify the trophic position of the individual, whereas stable carbon isotopes are used to trace the dietary carbon sources from primary producers. Results are expressed in standard δ notation based on international standards [39]. Stable isotope ratios are then reported in terms of the standard $\delta$ notation as units of parts per mil (‰) relative to the international reference standards used, which are the Vienna PeeDee Belemnite for 13C and atmospheric N2 for 15N (precision: 0.1‰) [33].

Stable isotope analyses were performed for fish and the cuttlefish *Sepia officinalis* from the Bay of Saint-Brieuc on the French side of the English Channel [33]. Refs. [41,42] analyzed the stable isotope signals (δ13C and δ15N) of the faunal communities associated with a wind turbine extensively colonized by the jassid amphipod *Jassa herdmani* (Walker, 1893), its scour protection layer (SPL) and the surrounding soft sediments. Subsequently, ref. [42] studied the attraction–production hypothesis of offshore wind farms through a combination of analyses of stomach contents and stable isotopes on fish surrounding the turbines. This method was also used by [43] to determine the prey of gray whales by studying the isotopic composition of the epidermis of Bering Sea whales. Recently, ref. [30] studied the diet of the pink cusk-eel fish *Genypterus blacodes* (Forster, 1801) in the southwestern Atlantic along the Argentine coast by combining analyses of stomach contents and stable isotopes.

### *2.5. Molecular Tools*

Ref. [44] used molecular tools, particularly sequencing (next-generation sequencing) platforms, to help understand the prey preferences and nutrient requirements of the wild paralarvae of cephalopods. These authors [44] aimed to determine the diet of paralarvae of the loliginid squid *Alloteuthis media* (Linnaeus, 1758) and enhance our knowledge of the diet of recently hatched *Octopus vulgaris* Cuvier, 1797, paralarvae.

Likewise, ref. [36] examined the potential consumption of amphipods by the dunlin *Calidris alpina* (Linnaeus, 1758), the semipalmated sandpiper *C. pusilla* (Linnaeus, 1766), the least sandpiper *C. minutilla* (Vieillot, 1819) and the short-billed dowitcher *Limnodromus griseus* (Gmelin, 1789) during spring migration through Delaware Bay using the amplification of prey DNA fragments in feces with amphipod-specific primers.

Recent progress in DNA-based tools has led to non-invasive approaches offering a more comprehensive and accurate characterization of animal diets. In this way, ref. [35] used a non-invasive metabarcoding approach to characterize the diet of the Westland petrel (*Procellaria westlandica*), an endangered burrowing species endemic to the South Island of New Zealand. Similarly, ref. [45] studied the diet of the black croaker fish (*Atrobucca nibe* (Jordan and Thompson, 1911)) in the southern coastal waters of Zhejiang Gan Chen (China), based on stomach contents and DNA analysis.

### *2.6. Caging Experiment*

To assess a potential trophic cascade, ref. [46] conducted a manipulative field experiment combining the effects of the shorebird *Calidris pusilla* and the eastern mud snail *Nassarius obsoletus* (Say, 1822) on the amphipod *C. volutator*. Caging was implemented on an intertidal mudflat community in the upper Bay of Fundy, New Brunswick, Canada, from June to September 2007. Previously, and in the same area, ref. [47] investigated the presence of a trophic cascade in the mudflat community during the period when shorebirds are abundant. For this purpose, they used a series of bird exclosures and the addition of fertilizer to examine top-down and bottom-up effects. These exclosures prevented birds from feeding and were compared with a paired control of zones where birds fed freely.

Similarly, ref. [48] conducted a predator exclusion experiment using an experimental design to compare the vertical distribution of *C. volutator* adults in areas with and without predation by the sandpiper *Calidris pusilla* Linnaeus, 1766. They set up the experiment in July 2007 at Pecks Cove in the Bay of Fundy, New Brunswick, Canada, an intertidal mudflat supporting migrating sandpipers each summer.

As a complement to laboratory experiments, ref. [49] used field experiments to test prey/predator relationships in the presence or absence of macro-algae at the Radio Island jetty in Beaufort, North Carolina (United States) during the summer of 1983. All 60 cages of the experiment were suspended 20 cm above the sediment surface to exclude non-swimming consumers. After three days, the algae and amphipods were counted.

In Western Australia, ref. [50] tested the possibility that resource limits might constrain the growth of mobile epifaunal populations associated with *Sargassum patens* plants by placing plants and associated animals into field microcosms that excluded fish predators. Predation by the most common fish species in the area, the wrasse *Halichoeres tenuispinis* (Günther, 1986), did not appear to alter macrofaunal production in the *S. patens* bed, but it nevertheless greatly affected the faunal size structure by eliminating most of the larger animals.

Ref. [51] used cages during the summer of 2009 to test the effects of fish predation on the amphipod assemblage structure of *Posidonia oceanica* (Linnaeus) Delile, 1813, meadows in a protected area in northeastern Sardinia. The experimental design consisted of three different treatments (uncaged areas, partially controlled cages and predator exclusion cages). Uncaged areas were made up of unmanipulated plots of *P. oceanica* seagrass meadow.

### *2.7. Laboratory Experiments*

Ref. [12] was one of the pioneers using laboratory experiments to test the relationship between amphipods and predators. Ref. [12] experimentally studied the relationship between the amphipods associated with eelgrass (*Zostera marina* Linnaeus, 1753) and the common predators of this habitat in the vicinity of Beaufort, North Carolina, United States. Two main predators were used: the shrimp *Palaemonetes vulgaris* (Say, 1818) and two size classes (small and large individuals) of the pinfish *Lugodon rhomboides* (Linnaeus, 1766). All the experiments used the amphipods *Melita appendiculata* (Say, 1818) and *Elasmopus levis* (S.I. Smith in Verrill, 1873). Depending on their availability, other amphipods were also tested as prey, including *Cymadusa compta* (S.I. Smith in Verrill, 1873) and *Ampithoe longimana* (Smith, 1873). *Melita appendiculata* was used as prey for all the experiments with pinfish.

Laboratory experiments were conducted by [52] to measure the prey selectivity of the fringed filefish *Monacanthus ciliates* (Mitchill, 1818). The prey included three species of gammarid amphipod, *Elasmopus levis* (S.I. Smith in Verrill, 1873), *Dulichiella appendiculata* (Say, 1818) (Melitidae) and *Bemlos unicornis* (Bynum and Fox, 1977) (Aoridae), using different combinations. The experiments showed that *B. unicornis*, a strikingly pigmented species, is over-consumed by filefish when placed in experimental aquaria with equal numbers of either *E. levis* or *D. appendiculata*, suggesting that this species is more accessible to predation due to its pigmentation.

Later, ref. [53] measured the fish predation of the shiner perch *Cymatogaster aggregata* Gibbons, 1854, on two species of caprellid amphipod (*Caprella laeviuscula* Mayer, 1903, and *Deutelia californica* Mayer, 1890) in the laboratory with the aid of microcomputer analysis of video-images. This technique allows the determination of prey preferences when the predator is exposed to multiple prey specimens exhibiting multiple prey behaviors.

To identify the trophic role of the amphipod *Jassa herdmani* (body length > 6 mm), individuals were collected from the fouling assemblages of Belgian Offshore Wind Farms (OWFs) [41]. Only female individuals were selected for the experiments. Two different food treatments were provided with six replicates: an algae diet providing powder of dried *Ulva* thalli (oven-dried for 5 h at 50 °C; dry weight ≈ 0.3 g) and an animal diet treatment using live freshly hatched *Artemia nauplii* (wet weight ≈ 0.07 g). Then, clearance rates and fecal-pellet carbon (FPC) were measured to estimate the role of this suspension-feeder amphipod.

To test the appetence of cuttlefish hatchlings feeding on amphipods, ref. [54] used a flow-through system composed of nine rectangular tanks with low light intensity to maintain low stress levels. The experiment lasted 21 days, corresponding to the hatchling stage when hatchlings are usually fed live prey entirely sufficient to ensure their diet.

In parallel with the field caging experiment, ref. [48] conducted laboratory experiments in the summer to examine the behavior of *C. volutator* females in the presence or absence of pecking designed to imitate the sandpiper *Calidris pusilla*. [48], simulating the pecking treatment to mimic natural shorebird predation behavior during the first five minutes immediately after low tide at a rate of one peck per second with a probe (2-mm diameter) inserted into the mud to a maximum depth of 5 mm.

Another type of laboratory experiment has been developed using macro-algae from intertidal and shallow water habitats since these seaweeds protect the vagile epifauna—including the amphipods—from predation by fish. In this context, ref. [49] tested in the laboratory the hypothesis that phytal amphipods were less susceptible to predation by fish when on highly branched, morphologically complex algal hosts than when on seaweeds with a simple bladed morphology. In their experiments, they used the amphipod *Ampithoe longimana* as the prey and the pinfish *Lagodon rhomboides* (Linnaeus, 1766) as the predator, with a combination of several branched and simpler sheet-like morphology seaweeds. In the same vein, seaweeds such as *Caulerpa racemosa* var. *cylindracea*, which are invading Mediterranean marine, vegetated habitats, can affect habitat structure [55]. These authors tested the effects of changes in habitat structure resulting from colonization by *C. racemosa* on prey availability for predators. In laboratory experiments, they assessed the importance of amphipods as a trophic resource in natural vegetated habitats. They investigated the influence of this alien alga on predation by the ornate wrasse *Thalassoma pavo* (Linnaeus, 1758) feeding on two amphipod species: *Elasmopus brasiliensis* (Dana, 1853) and *Caprella dilatata* Kröyer, 1843.

## 3. Birds

### 3.1. Shorebirds

An uncommon behavior of the varied thrush *Ixoreus naevius* (Gmelin, 1789)—a bird living primarily in the dense, humid forests of western North America from California to Alaska—has been observed in the case of two individuals feeding actively above the high tide mark on an open sandy beach by [56]. The two birds were observed consuming a large number of sand-hopper amphipods of the family Talitridae, mainly *Megalorchestia californiana* Brandt, 1851, and *Traskorchestia traskiana* (Stimpson, 1857), which inhabit sand beaches of the Olympic National Park Ocean–beach wilderness strip in Clallam County, Washington, DC, USA.

The data on shorebirds are well documented. Ref. [34] studied the winter feeding of the Turnstone in North Wales, UK, showing that this shorebird eats amphipods as a preferred prey until they become harder to find. Although some amphipods in the pellets were unidentifiable, they were presumed to belong to the genus *Gammarus* and *Marinogammarus*, while others could be assigned to the species *Talitrus saltator* (Montagu, 1808). Evidently, these birds preferred to feed on amphipods (perhaps the most productive food source in the locality), but as these became less available, the birds changed their feeding behavior to take other prey and so became less specialized.

The amphipod *C. volutator* is one of the most abundant amphipod species on the mudflats of European and North American estuaries, and its role in the diet of shorebirds has been illustrated in numerous studies [57–63]. Predation by shorebirds induces changes in the densities and sizes of the amphipods, with the adults becoming more strongly predated, while the populations show an increase in juveniles. The changes in behavior are associated with a deeper penetration in the sediment when the predation is strong. But *C. volutator* is a resilient species, able to rapidly reconstitute its population when the predation ceases due to shorebird migration.

It has been shown that the redshank *Tringa totanus* (Linnaeus, 1758) feeds more intensively on the Ythan and the Forth estuaries in northeast Scotland, where the amphipod *C. volutator* is highly abundant. Correlations have been established between areas with dense *C. volutator* populations and nourishing areas of *T. totanus* at low tide [64,65]. Ref. [60] examined the possible impact of intense periodic predation by the sandpiper *Calidris pusilla* on the life history patterns of its amphipod prey, *C. volutator.* These authors focused their study on two mudflats in northeastern Nova Scotia, Bay of Fundy, Canada; one site was annually visited by the shorebirds and the other not. On the mudflat not visited by sandpipers, densities increased during the spring and then remained constant through the summer with continuous reproduction. A mid-summer decrease in amphipod abundance on the mudflat visited by sandpipers could not be attributed directly to sandpiper predation; moreover, selective predation on large amphipods contributed to a second peak in abundance by increasing juvenile survivorship due to the removal of competing adults.

Using caging experiments, ref. [46] studied the interactions between three species: the shorebird *Calidris pusilla* (Linnaeus, 1766) as a predator of the amphipod *C. volutator* and the eastern mud snail as a benthic competitor. Snails exhibit density-dependent top-down effects, primarily derived from strong negative interactions with juveniles and adult *C. volutator* that are likely due to interference, consumption and emigration. Shorebirds are less influential in determining community structure. They reduce *C. volutator* biomass through consumption, but there is no resulting effect on primary production. The top-down effects of snails and birds are cumulative on *C. volutator*, but they do not generate a trophic cascade. This experiment confirms the previous results of [47,66] from the same site on the upper Bay of Fundy, Canada, which revealed negative interactions between *C. volutator*

(Pallas), with the eastern mud snail, *N. obsoletus*, as both species utilize similar habitats and food resources.

Ref. [48] carried out field and laboratory experiments to study the relationship during the summer between the tube-dwelling amphipod *C. volutator* and its natural predator the sandpiper *Calidris pusilla* in Pecks Cove (Bay of Fundy, New Brunswick, Canada). These studies show stronger predation on amphipods in areas exposed to bird predation than in bird enclosures. During peak predation, many *C. volutator* adults burrow beyond the reach of feeding sandpipers (1.5 cm deep). This observed reorganization of behavior suggests that *C. volutator* adults move deeper into their burrows as an anti-predator response to the presence of sandpipers.

Amphipod DNA was found to be present in fecal samples of the four shorebird species studied by [36], with non-significant differences among species in 2011. Amphipod DNA was detected in 31% of the semipalmated sandpipers, 67% of least sandpipers, 17% of dunlins and 50% of short-billed dowitchers. In 2012, significant differences in the consumption of amphipods were observed: amphipods were detected in 49% of semipalmated sandpipers, 91% of least sandpipers, 0% of dunlins and 71% of short-billed dowitchers [36]. Nevertheless, this molecular approach does not allow us to identify which amphipod species are predated.

More generally, studies on intertidal sand and mud flats around the Atlantic and Pacific have shown that these habitats play an important part in the nourishment of shorebirds, such as in Scotland [64,65], Wales [34], the Bay of Fundy, Canada [46–48,60,66], Oregon, USA [61] and Baja California, Mexico [67].

In the North of France, ref. [68] studied the temporal changes in intertidal macrobenthic communities and the occupation of shorebirds on a beach near Calais between the autumns of 1982 and 2010. Trends observed for the dunlin *Calidris alpina*, gray plover *Pluvialis squatarola* (Linnaeus, 1758) and sanderling *Calidris alba* (Pallas, 1764) at the study site were consistent with the patterns observed in global flyway populations. Ref. [68] stresses that the rise of the sanderling is locally related to the spatial extension of the amphipod and polychaete community in littoral-medium fine sands (+55% between 1982 and 2010). This benthic community hosted a higher number of shorebirds in 2010 (+32%) and provided an important food resource for sanderlings: among the amphipods, the high abundance of *Bathyporeia* spp. suggests that this species is an important prey for shorebirds. Their study reveals that the construction of a seawall between 1982 and 2010 led to a major spatial reorganization of the macrobenthic communities, with a drastic reduction of the muddy-sand community. However, no clear relation could be detected between macrobenthic changes and shorebird abundances.

### *3.2. Other Birds*

Some studies have focused on Arctic Ocean birds. For example, ref. [69] examined the diet of the black guillemot *Cepphus grille* (Linnaeus, 1758) in the eastern Canadian Arctic via the analysis of stomach contents and foraging habitat selection. This bird feeds mainly on fish and mysids, as well as on amphipods and decapod crustaceans. Crustaceans are represented in 56.5 and 54.5% of stomachs, mysids being the most frequently identified crustaceans. Amphipods are less numerous but more diverse, with benthic *Gammarus* being one of the most represented genera. Four benthic species, *Gammarus setosus* Dementieva, 1931, *Ampelisca macrocephala* Liljeborg, 1852, *Apherusa glacialis* (Hansen, 1888) and *Onisimus nanseni* (G.O. Sars, 1900), have been identified in black guillemot stomachs. Later, ref. [28] studied the diets of the common and Briinnich's guillemots *Uria aalge* and *U. lomvia* in the Barents Sea region. The stomach contents of adult Briinnich's guillemot indicate that polar cod and crustaceans (mainly amphipods) are the most frequent items taken during the breeding season. Among the amphipods, *Gammarus* ssp. And, in particular, *G. locusta* (Linnaeus, 1758) is preferentially consumed. However, prior to and after breeding, the diet of Briinnich's guillemot reported in or near the ice edge consists almost entirely of crustaceans dominated by the benthic *Gammarus* spp.

In the Bering Sea, the effects of gray whale feeding provide a food source for surface-feeding birds [70]. To identify the interactions between two top predators, seabirds and whales, ref. [70] studied the diet of four seabirds collected in the immediate vicinity of whale slicks sampled using neuston tows: the red phalarope *Phalaropus fulicarius* (Linnaeus, 1758), the northern fulmar *Fulmarus glacialis* (Linnaeus, 1761), Brünnich's guillemot *Uria lomvia* and the black-legged kittiwake *Rissa tridactyla* (Linnaeus, 1758). A total of nine amphipod taxa were found in their stomachs, with a high occurrence of Ampeliscidae *Ampelisca* and *Byblis* in the four bird species and a net difference between the diet of *Uria lomvia* and the diets of the other three birds.

Ref. [71] studied the diet of six seabirds in the Svalbard area during the spring and summer seasons between 1982 and 1990: the northern fulmar *Fulmarus glacialis*, black-legged kittiwake *Rissa tridactyla*, ivory gull *Pagophila eburnea* (Phipps, 1774), Brunnich's guillemot *Uria lomvia*, black guillemot *Cepphus grille* (Linnaeus, 1758) and little auk *Alie alle* (Linnaeus, 1758). Most seabirds were collected at sea. All specimens shot were fully grown individuals, and their stomachs and esophagus tracts were examined to identify the consumed prey. Benthic gammarids were found in four seabird species: the kittiwake, both guillemots and the little auk, accounting for up to 40% occurrence in the stomachs. Four benthic amphipods were identified: *Anonyx nugax* (Phipps, 1774), *Apherusa glacialis* (Hansen, 1888), *Gammarellus homari* (J.C. Fabricius, 1779) and *Gammarus wilkitzkii* Birula, 1897.

The most complete study so far in the Antarctic Ocean was carried out by [2], who examined the diet of 27 seabird species from the Sub-Antarctic Crozet Islands in the southern Indian Ocean. Among the 22 amphipods identified as prey, eight were pelagic hyperiids. Among the benthic species, *Eurythenus obesus* showed the highest occurrence (found in seven seabirds), followed by *Eurythenus gryllus* in four seabirds, while the other benthic amphipods were found in only one or two species of seabird.

The diet of the emperor penguin *Aptenodytes forsteri* G. R. Gray, 1844, in the western Ross Sea during spring was investigated via the analysis of stomach contents sampled at three different localities [72]. Emperor penguins' prey on fish (89 to 95% of the biomass) and crustaceans (5 to 11%). The most diverse and abundant taxon is represented by the Amphipoda. The crustacean part of the diet was dominated by the gammarid amphipods *Abyssorchomene rossi* (Walker, 1903), *A. plebs* (Hurley, 1965) (both species accounting for 30% of the crustacean prey) and *Eusirus microps* Walker, 1906 (22%). Other amphipods were found in the stomach contents but with low occurrences, including the benthic species *Eusirus propeperdentatus* Andres, 1979 and *Uristes gigas* Dana, 1852. Most of the amphipods were >20 mm in total length, the largest species being *Eusirus* spp.

Ref. [73] studied the amphipod crustaceans in the diet of three breeding pygoscelid penguins of King George Island, South Shetland Islands, Antarctica, the Adelie penguin *Pygoscelis adeliae* (Hombron and Jacquinot, 1841), the chinstrap penguin *P. antarcticus* (Forster, JR 1781) and the Gentoo penguin *P. papua* (Forster, JR 1781), in the vicinity of the Polish Arctowski Station during the austral summer 1977/1978. In all, 123 penguins (48 specimens of *P. adeliae*, 29 of *P. antarctica* and 46 of *P. papua*) were dissected, showing that amphipod crustaceans were present in the stomachs of 26 of them (22% of all samples): 15 individuals of *P. adeliae*, 5 of *P. antarctica* and 6 of *P. papua.* Amphipoda were found in 31% of the stomachs, including 10 gammarid. About 15% of all amphipod specimens found in the penguin stomachs were benthic species that are very common in Antarctic coastal waters and that probably swarm.

Using a non-invasive DNA metabarcoding approach, ref. [35] recognized the presence of talitroidean amphipods in the diet of the Westland petrel *Procellaria westlandica* from the South Island of New Zealand.

## 4. Cephalopods

The cuttlefish is a very common species along the Atlantic coast of France and in the English Channel. A nursery ground of *Sepia officinalis* (Cephalopoda: Sepiidae) has been identified in the Gulf of Morbihan in France, as well as in the northern part of the Bay of

Biscay, and their abiotic and biotic features, such as growth and development, have been monitored over a period of five months [31]. The analysis of stomach contents and the identification of the prey consumed showed that crustaceans (mainly amphipods, as well as brachyuran and macruran decapods) made up the diet of young cuttlefish. Some species, such as the Caprellidae *Phtisica marina* Slabber, 1769, are present in large quantities in the stomachs of young cuttlefish, with as many as 24 specimens in one stomach. Two other hard-bottom amphipods, *Dexamine spinosa* (Montagu, 1813) and *Chaetogammarus marinus* (Leach, 1816), and one soft-bottom amphipod, *Ampelisca brevicornis* (A. Costa, 1853), formed part of the diet in June. From July to September, some amphipods (*Phtisica marina*, *Ampelisca brevicornis* and *Chaetogammarus marinus*) were found in the stomachs, but their frequency decreased with the increasing size of the cuttlefish.

The diet of *S. officinalis* in Southern Moroccan Atlantic waters was studied by ref. [32] between Cap Boujdour and Cap Blanc during an annual cycle between September 2013 and October 2014. Fish (51%) and crustaceans (43%) were the dominant prey category, while cannibalism represented 14% of the prey. The main prey of juveniles were shrimps, amphipods and isopods.

Ref. [33] used stomach contents and stable isotope analyses to show that the diet of young cuttlefish collected in September 2019 from the Bay of Saint-Brieuc (the French side of the western English Channel) was dominated by Caridea (46%) and fish (51%), while amphipods were consumed only during the first stages of development of this species.

The diet composition and variability of the wild *Octopus vulgaris* and *Alloteuthis media* paralarvae were investigated with metagenomic analyses by [44], who identified 122 molecular taxonomic units (MOTUs) belonging to several taxa of decapods, copepods, euphausiids, amphipods, echinoderms, mollusks and hydroids.

With a view to developing the aquaculture of *S. officinalis*, several experiments have been carried out to test the appetency of cuttlefish for amphipods. In this context, ref. [54] tested the effects of feeding exclusively caprellids (*Caprella equilibra* Say, 1818) or three gammarids (*Ericthonius brasiliensis* (Dana, 1853), *Jassa marmorata* Holmes, 1905, and *Elasmopus* sp.) to cuttlefish hatchlings. This prey was compared to feeding with mysids alone (*Mesopodopsis slabberi* (Van Beneden, 1861)), which are normally used in the experimental design during the first weeks of the life cycle. Cuttlefish hatchlings fed with mysids and gammarids grew faster compared to caprellids. Survival was higher for hatchlings fed on mysids compared to those fed on gammarids and caprellids, respectively. The [54] study revealed a successful use of amphipods, mainly gammarids, as an alternative prey for cuttlefish hatchlings

## 5. Fish

Bentho-demersal fish are known to be opportunist predators that feed on various benthic organisms (Appendix A). Nevertheless, a comparison between available and consumed macrobenthic prey found in fish stomachs showed that some taxa are over-consumed, while others are under-consumed (Table 1) [18,74].

The endofauna living at several centimeters' depth in the sediment, such as certain mollusks and polychaetes, are among the under-consumed prey. Conversely, epifauna living in the topmost few centimeters of the sediment and at its surface are over-consumed. Among the crustacean decapods and peracarids, the amphipods appear as the preferential prey of numerous fish. Moreover, the predation on these benthic species is increased due to the fact that they perform diel migrations, staying on the sea bottom during the day and moving into the benthic boundary layer and the water column during the night [8]. Correlatively, suprabenthic species are undoubtedly more accessible to fish during the night-time, mainly at sunset and sunrise, when these species are most mobile [9]. High abundances of clupeid larvae in the benthic boundary layer have been observed in the eastern part of the Bay of Seine, probably to feed on emergent crustacean species at these particular moments [7].

**Table 1.** Mean composition of the vagile epifauna and the infauna of the macrobenthos sampled with a Smith McIntyre grab (10 replicates of 0.1 $m^2$) in November 1977 and from April 1980 to April 1981 and the number of preys identified in the stomach contents of demersal fish sampled on the fine sand of the Bay of Morlaix, the English Channel (number of individuals per category standardized to 1000) [18].

| | **November 1977** | | **April 1980 to April 1981** | |
|---|---|---|---|---|
| | **Grab** | **Stomach** | **Grab** | **Stomach** |
| Polychaeta | 93.4 | 16.7 | 520.8 | 131.0 |
| Bivalvia | 4.3 | 62.8 | 105.6 | 42.1 |
| Gastropoda | 0.3 | 0 | 3.9 | 0.4 |
| Ophiuroidea | 1.49 | 12.6 | 7.9 | 7.1 |
| Natantia Decapoda | 0.4 | 146.0 | 2.3 | 117.7 |
| Macroura Decapoda | 0 | 8.4 | 0.05 | 1.3 |
| Brachyoura Decapoda | 0.3 | 25.1 | 0.6 | 30.6 |
| Anomoura Decapoda | 0.1 | 25.1 | 1.1 | 46.6 |
| Cumacea | 0.1 | 0 | 1.5 | 4.0 |
| Isopoda | 0.2 | 12.6 | 0.6 | 1.1 |
| *Ampelisca* spp. | 887.1 | 631.8 | 252.4 | 152.3 |
| Other Amphipoda | 10.3 | 54.4 | 99.4 | 392.1 |

The following examples selected here illustrate the relationships between fish as predators when amphipods act as accessory, accidental or preferential prey species. The high diversity of benthic amphipods is related to the numerous bentho-demersal fish that feed on this available prey.

Ref. [75] has studied the amphipod species consumed by the pinfish in three seagrass habitats in Apalachee Bay, Florida (USA). In this case, predatory preferences were more closely linked to the microhabitat of prey species but unrelated to amphipod abundances. The consumption of preferred amphipod species appeared non-selective at a site with sparse macrophyte cover, but it selectivity increased with macrophyte biomass.

Ref. [76] studied feeding site selection and the effects of demersal fish predation on the amphipod *C. volutator* from mudflats in Nova Scotia, Canada. Fish preferentially consume more juvenile amphipods and more males than females. Daily foraging pressure by fish was found to be low (about 0.3% per day), while fish predation had an important impact on the demography of *C. volutator* due to the length of the fish foraging season. Moreover, fish appeared to contribute to the severely female-biased sex ratio typically observed in this amphipod species. These results were confirmed by [77], who studied the intense episodic predation by shorebirds in the Bay of Fundy. They showed that selective predation on older or larger individuals in populations of *C. volutator* should lead to a smaller size at maturity and a tendency toward semelparity. They demonstrated that this intertidal amphipod can adapt its reproductive strategy under intense predation by fish.

In the English Channel, one of the first studies of the relationship between benthic communities and the food of fish was carried out by [16] in the shallow waters of offshore Plymouth, Cornwall, United Kingdom. He found amphipods in five demersal fish: the gurnard *Trigla lineata* Gmelin, 1789, the common dragonet *Callionymus lyra* Linnaeus, 1758, the young plaice *Pleuronectes platessa* (Linnaeus, 1758), the ray *Raja clavata* Linnaeus, 1758 and *R. maculata* Shaw, 1804.

Ref. [18] studied the importance of predation by 13 demersal fish in the fine sand community of the Bay of Morlaix, on the French side of the English Channel, dominated by the amphipod *Ampelisca* spp., using stomach content analysis in relation to the macrobenthic fauna. Three small species, *Trisopterus minutus* (Linnaeus, 1758), *Callionymus lyra* and

*Echiichthys vipera* (Cuvier, 1829), are the most abundant benthic fish. Fish feed on the macrobenthic fauna, especially crustacean amphipods, while polychaetes and bivalves are only secondary prey. Moreover, ref. [18] showed that the fish adapted their food items in relation to the prey available after the Amoco Cadiz oil spill, which destroyed the populations of hydrocarbon-sensitive *Ampelisca* (Table 1). In the Bay of Saint-Brieuc, ref. [33] used stomach contents and stable isotopes to show the importance of amphipoda as prey for six fish: the main prey for *Buglossidium luteum* (Risso, 1810), *Mullus surmuletus* Linnaeus, 1758, and *Spondyliosoma cantharus* (Linnaeus, 1758) and a secondary prey for *Arnoglossus laterna* (Walbaum, 1792), *Callionymus lyra* and *Gobius niger* Linnaeus, 1758. The studies of the stomach contents of demersal fish in the eastern basin of the English Channel, in the Bay of Seine [78,79] and along the Opal Coast [74,80], allow us to compare the consumed prey at three shallow sites (Appendix A). These studies showed that amphipods are predated in the shallow waters of the English Channel by demersal fish, but the consumed species vary from one area to another. In the Bay of Morlaix in the western part of the English Channel, *Ampelisca* spp. is the preferential prey, while *Apherusa bispinosa* (Spence Bate, 1857) and *Megaluropus agilis* Hoek, 1889, are the main prey in the eastern part of the English Channel, showing that fish are opportunist and consume the dominant amphipods available.

According to [81], the dominant amphipod *Caprella laeviuscula* resident in the *Zostera marina* seagrass meadows of Padilla Bay, Washington, western Pacific Ocean, USA, shows an abundance reaching > 93 individuals per 625 $cm^{-2}$ during winter. When shiner perch *Cymatogaster aggregata* invade the seagrass in reproductive migrations, caprellid abundances drop to < two individuals per 625 $cm^{-2}$. Although caprellids normally do not represent a major item in fish diets, shiner perch seem to preferentially prey upon the caprellids immediately following immigration into the seagrass beds.

The diets of seven deep-benthic skates were examined by analyzing the stomach contents of fish collected in deep waters off the northern Kuril Islands and southeastern Kamchatka in the North Pacific [82]. The diet of predatory Alaska skate *Bathyraja parmifera* (Bean, 1881) and *B. matsubarai* (Ischiyama, 1952), Aleutian skate *B. aleutica* (Gilbert, 1896) and white blotched skate *B. maculata* Shiyama and Ishihara, 1977, consisted mainly of large crustaceans, cephalopods and worms. Benthopelagic sandpaper skate *B. interrupta* (Gill and Townsend, 1897), Okkotsk skate *B. violacea* (Suvorov, 1935) and brown skate *B. minispinosa* Ishiyama and Ishihara, 1977, consumed mainly amphipods and worms. The amphipods were found in the diet of the seven species, but their occurrences declined with an increasing skate size.

Ref. [22] studied the diet of three species of rays, *Raja brachyura* Lafont, 1873, *R. clavata* and *R. montagui* Fowler, 1910, from the Bay of Douarnenez in the northern part of the Bay of Biscay. In the south of the Bay of Biscay, ref. [19] determined the diet of 34 demersal fish from the continental shelf and top of the Atlantic continental slope in offshore Arcachon, France, via the analysis of the digestive contents. The small motile benthic crustaceans (Mysidacea, Amphipoda, young natantian and brachyuran decapods) were the most important food for the euryphagous fish during the first years of their life near the sea bottom. Twenty-four species of amphipods were found in the stomachs of 23 fish out of the 34 examined, representing 17% of the total prey consumed. Four amphipod species were distinguished by the total number of individuals recorded and the number of their predators: *Hippomedon denticulatus* (Spence Bate, 1857), *Ampelisca brevicornis* (A. Costa, 1853), which was a preferred prey for Soleidae *Solea vulgaris* Quensel, 1806, *Pegusa lascaris* (Risso, 1810), *Dicologlossa cuneata* (Moreau, 1881) and *Kroyera carinata* Spence Bate, 1857, which were actively sought by *Mullus surmuletus* and *Westwoodilia caecula* (Spence Bate, 1857) and consumed by *Chelidonichthys lucerna* (Linnaeus, 1758). The trophic role of amphipods was only really noticeable in six demersal fish: *Capros aper* Linnaeus, 1758, *Mullus surmuletus*, *Chelidonichthys obscurus* (Walbaum, 1792), *Solea vulgaris*, *Pegusa lascaris* and *Dicologlossa cuneata*.

Ref. [83] studied the predation of the cod *Gadus morhua* Linnaeus, 1758, on amphipod crustaceans in the northwestern Atlantic. During research cruises between 1979 and 1992, a total of 297 of cod were caught containing amphipods. Most individuals were obtained in the spring (March–May) and caught at depths between 40 to 450 m. Cod with amphipods ranged in length from 20 to 126 cm, but most of them were 30 to 70 cm; the benthic prey diminished with the size of the cod. Moreover, 82 species of amphipods (76 Gammaridea, 2 Caprellidea and 4 Hyperiidea) were identified in the stomachs. A few species were found in cod at all depths, but most occurred in depth-defined patterns. The authors [83] observed that mature amphipod males with morphological changes allowing a pelagic life in the water column were more abundant in cod stomachs than immature amphipods, which remained near the sea bottom.

Ref. [76] studied the effects due to predation of the flounder *Pseudopleuronectes americanus* (Walbaum, 1792) and the ray *Leucoraja ocellata* (Mitchill, 1815) on the intertidal amphipod *C. volutator* which adapt is behavior seasonally [84], from Starrs Point a mudflat in the northeastern Bay of Fundy, Canada. All flounders were of adult size, and all rays were subadults. The gut contents of both fish yielded moderate to large numbers of *Corophium*.

From stomach contents and DNA extraction, ref. [45] identified several amphipods as prey in the diet of black croaker in the southern coastal waters of Zhejiang, China; the gammarideans *Ampelisca* spp. and *Monoculodes* spp. were identified only via stomach content analysis.

Experiments in the field and in the laboratory on prey/predator relationships in the presence of macro-algae have shown that the amphipod *Ampithoe longimana* is more susceptible to predation by the pinfish in highly branched seaweeds than species with a simpler sheet-like morphology [49]. Similarly, Mediterranean *Posidonia oceanica* seagrass meadows are potentially relevant trophic resources for ichthyofauna. Ref. [51] carried out experimental manipulations of predation intensity (exclusion and inclusion cages) at two sites in a Sardinian marine protected area with different levels of fish predation. In the absence of predatory fish (exclusion cages), total amphipod density and biomass were found to be higher than in uncaged areas and partially controlled cages. At the species level, *Caprella acanthifera* Leach, 1814, and *Iphimedia minuta* G.O. Sars, 1883, responded to caging by showing increased abundance. The presence of one enclosed labrid fish predator (inclusion cages) resulted in a lower density and biomass of *Aora spinicornis* Afonso, 1976, and a lower biomass of *Phtisica marina*, although total amphipod density and biomass were unchanged. In the experiments with inclusion cages, size frequency analysis revealed that predators mainly targeted large individuals of *A. spinicornis* and *Apherusa chiereghinii* Giordani Soika, 1950.

Ref. [55] experimentally studied the consumption of the labrid fish *Thalassoma pavo* living in several algae habitats, including those of the invasive alien species *Caulerpa racemosa* var. *cylindracea*. The highest predation rate was found in the habitat of this latter alien species. The pattern of predation across habitats, however, was similar for both caprellid and gammarid amphipods, indicating a more general effect of habitat on amphipod predation.

## 6. Mammals

The predation of the gray whale *Eschrichtius robustus* on the dense ampeliscid populations along the northwestern Pacific Ocean coast from Baja California in the south to the Bering Sea in the north has been remarkably documented over the past four decades for gray whales and walruses [37,85–87]. The first observations were made with scanning sonar, which revealed the presence of numerous oval pits in shallow waters [88]. Researchers were fascinated by these regular forms on the sea bottom and later found that they were due to the benthic scavenging of gray whales feeding on dense ampeliscid populations [86–88]. However, ref. [86] suggested that the feeding of gray whales on benthic invertebrates was not common in Baja California.

The feeding behavior of the gray whale is unique among the baleen whales. Infaunal prey communities and gray whale feeding excavations have been found at three sites along the west coast of Vancouver Island: Ahous Bay, Pachena Bay and Port San Juan [88]. In these areas, side-scan sonar records have indicated that whales disturb up to 36% of the sea floor with about 17% of the bottom covered with feeding excavations. Moreover, these authors [88] showed that there was a positive correlation between the biomass of ampeliscid amphipod prey and the total quantity of prey consumed by gray whales at the three feeding grounds. They observed two types of gray whale excavations: large complex excavations (mean > 20.5 $m^2$) and small pits (mean < 4 $m^2$). In fact, gray whales expand the small feeding excavations into large, complex features by feeding along the edges of existing depressions. Gray whale feeding suspends over 1000 $m^3$ of sediment per day. *Ampelisca* spp. could rapidly colonize the excavations, thus showing a highly resilient behavior [88].

Gray whales suck sediment and fauna into their mouths, capturing prey on the baleen filter, and then expel sediment through the baleen [85,86]. Later, large feeding excavations (often 2–20 $m^2$) are rapidly colonized by scavenging lysianassid amphipods, especially *Anonyx* spp., that attack injured and dislodged infauna [87]. Ref. [87] carried out field studies indicating that benthic amphipods brought to the surface during gray whale feeding provide a food source for surface-feeding birds [70,89]. In this way, the gray whale participates in an ecological succession of benthic organisms in areas where the gray whale feeds, thus favoring a trophic cascade between amphipods and arctic birds. Similarly, in the Bering Sea, the walrus *Odobenus rosmarus* (Linnaeus, 1758) influences the structure of macrobenthic communities by excavation of their major bivalve prey from soft sediments. As observed with the gray whale, the pits formed by the walruses are colonized by lyssianasids [87].

The benthic communities of the Chirikov Basin in the northern Bering Sea are dominated by amphipods of two of the four genera of the Ampeliscidae family: *Ampelisca* and *Byblis* [26,90,91]. In the northern Bering Sea, five *Byblis* species and four *Ampelisca* species have been reported [92]: *B. gaimardii* (Krøyer, 1846), *B. brevirama* (Dickinson, 1983), *B. pearcyi* Dickinson, 1983, *B. frigidus* Coyle and Highsmith, 1989, and *B. robustus* Coyle and Highsmith, 1989, and *A. macrocephala* Liljeborg, 1852, *A. erythrorhabdota* Coyle and Highsmith, 1989, *A. eschrichtii* Krøyer, 1842, and *A. birulai* Brüggen, 1909.

Measurements in the 1980s indicated that the Chirikov Basin ampeliscids comprised one of the most productive amphipod communities of the worldwide Ocean [93], with maximum values comprised between 170 and 230 $kcal{\cdot}m^{-2}\ yr^{-1}$ and a mean dry weight biomass of 30–40 $g{\cdot}m^{-2}$. Dietary analysis indicated that ampeliscids were the primary prey item of this whale [94,95]. It was estimated that 87% of the *Eschrichtius robustus* population spent some time foraging in this area, and about 17% stayed for approximately 6 months of the year (May–October) in the Chirikov Basin to obtain most of their annual energetic requirements [27].

A decline of about 30% has been observed in the gray whale population, from about 30,000 individuals in 1997/1998 to 18,000 in 2001/2002. Ref. [91] suggested that, in the central Chirikov Basin, the abundance and biomass of the *Ampelisca* populations decreased during the 3-year period from 1986 to 1988, resulting in a 30% decline in production probably due to high predation by the gray whale. As pointed out by [27], the reasons for this decline in the gray whale population remain uncertain; however, while food limitation could be a potential cause, some evidence indicates that gray whales may be approaching the carrying capacity of their habitat. It has been suggested that, in the Chirikov Basin, the gray whale population might have a top-down control of the amphipod community. Moreover, climate-related changes in the Bering Sea ecosystem suggest that gray whale food resources might be impacted by global climate change. During two cruises per year between June and September in 2002 and 2003, ref. [27] resampled the 20 stations occupied during the 1980s to determine whether there had been any significant changes in Ampeliscidae abundance and biomass. During 2002–2003, the average Ampeliscidae dry weight biomass was about 28 $g{\cdot}m^{-2}$, a decline of nearly 50% from maximum values in the 1980s. Amphipod length measurements indicate that the decline is due mainly to the absence of larger individuals (20–30 mm length).

Refs. [95–97] reviewed the feeding ecology of gray whales from the Bering and Chukchi Seas. In this area, amphipods comprise approximately 95% of the diet of gray whales; out of the 43 species identified from stomach contents, seven species, *Pontoporeia femorata*, *P. affinis*, *Anonyx nugax*, *Ampelisca macrocephala*, *A. eschrichtii*, *Nototropis brueggeni*, and *N. ekmani*, depending on the area, are usually dominant in the diet. Gray whales also consume other large and small benthic invertebrates, epifaunal invertebrates in kelp forests and along rocky shores and zooplankton such as shrimps, crabs, polychaetes, snails, clams and isopods [97].

Based on isotopic analysis of the epidermis of gray whales living in the Bering Sea, ref. [43] inferred that only four females out of 25 could have fed in the primary feeding ground of the Bering Sea, while the others appear to have favored mysids from Vancouver Island (n = 15), or have integrated prey in both the Bering Sea and Vancouver Island (n = 5). This study confirms that the gray whale shows behavioral plasticity and does not feed solely on dense amphipod Ampeliscidae populations in the Pacific and Arctic.

Moreover, it is known that Arctic ampeliscids have slow growth rates and long generation times; therefore, the ampeliscid community might require several years or decades to recover to the densities observed in the 1980s. Predicted warming trends in the northern Bering Sea could impact ampeliscid recovery by lowering primary production or altering the community composition of the benthos [27].

The ability of gray whales to severely reduce benthic ampeliscid amphipod prey has been documented [27,98]. Moreover, the patterns of foraging intensity of gray whales (*Eschrichtius robustus*) were examined over a 17-year period (1997–2013) in Clayoquot Sound, Vancouver Island [98]. These authors [98] showed that, among the Peracarida, the epibenthic mysid species were the primary prey of gray whales and that summers with very high foraging contributed to reduced prey resources being available the following summer. Years of heavy predation pressure were followed by at least one year of reduced foraging, probably allowing a reprieve during which the mysids could repopulate.

Ref. [37] investigated habitat utilization and predation of the gray whale on benthic *Ampelisca* spp. and the pelagic *Atylus borealis* over 26 years, from 1989 to 1996. Whale distribution and movements were observed from March to November via boat surveys and whale-watch sighting programs, while prey species were collected via a suction hose and a plankton net or determined through the analysis of fecal samples. These authors identified that the whale prey species in this area included herring eggs and larvae, crab larvae, mysids, shrimps and amphipods, mainly the benthic *Ampelisca* spp. and the pelagic *Atylus borealis* Bousfield and Kendall, 1994. The *Ampelisca* was a common and important source of the diet for gray whales in the small bay on the shallow western coast of Vancouver Island [37].

Since the end of commercial whaling in the 1970s, the recovery of the western gray whale has been slow on the other side of the North Pacific Ocean along the Kamchatka coast, per ref. [99], compared with the eastern gray whale along the American coast. On the northeastern Sakhalin Shelf, gray whales feed mainly on the vast and dense populations of the amphipod *Ampelisca eschrichtii* Krøyer, 1842. The maximum density recorded here is 13,350 ind$\cdot$m$^{-2}$, with a biomass of 705 g$\cdot$m$^{-2}$ wet weight and a production of 1130 g$\cdot$m$^{-2}$ per year. In this area, *A. eschrichtii* populations seem to be limited due to western gray whale predation, but high production rates of the offshore ampeliscid populations provide significant potential to favor quick recovery from intense predation [98]. Since other feeding areas are likely to contain similar prey sources as the Sakhalin Island Shelf, the limited growth of the gray whale feeding aggregation off northeastern Sakhalin is unexpected in view of the fact that it nowadays comprises less than 200 individuals, while 1500–10,000 whales are estimated to have been in the region in the 19th century [99].

The gray whale could adapt its prey consumption due to the strong decline in the *Ampelisca* spp. population. During the period from 1999 to 2005, ref. [38] observed the presence of about 40–50 whales to the southeast of Kodiak Island, Alaska. These whales kept the same predation behavior on benthic communities dominated by cumaceans belonging to the Diastylidae family and associated with polychaetes and bivalves. Evidence that gray whales were consuming cumaceans resulted from the examination of fecal samples, which contained voluminous quantities of (usually partially digested) diastylids. This study illustrates the capacity of gray whales to exploit disparate forage opportunities and respond to environmental changes [38].

In Clayoquot Sound, Vancouver Island, British Columbia, gray whales forage benthic invertebrates, mainly the mysids and amphipods, which are largely dominated by *Ampelisca agassizi* (Judd, 1896) and *A. careyi* Dickinson, 1982, having an estimated biomass of 160 ± 150 g wet weight per square meter. In this area, whales forage where there are high proportions (61%) of amphipods > 6 mm in length [96]. These same authors found that whales initially forage for amphipods along the 20-m depth contour; amphipod biomass is maximal at depths between 16 and 20 m.

## 7. Impact of Offshore Wind Farms on the Trophic Chain

Nowadays, the wind farm industry has increased its activities dramatically in offshore marine areas and numerous coastal sectors in Europe, North America and Asia, mainly in China, which has achieved the highest growth of marine wind farms over the two last decades. This new marine activity is linked to the goal of developing renewable energy to attain carbon neutrality; moreover, the wind intensity is stronger at sea than on land and offers the opportunity for such energy development. The southern North Sea offshore from the coasts of Germany, the Netherlands, the United Kingdom and Belgium has been intensively equipped with offshore wind farms [100]. Each turbine is placed on a specific foundation type, with scour protection installed at the foot of the turbine to prevent sediment erosion. The submerged parts of these structures act as artificial reefs, providing new habitats and likely affecting fisheries' resources [41,100]. As for artificial reefs, the installation of an OWF is invariably followed by the rapid colonization of all the submerged parts by a variety of fouling organisms.

The impact of OWF development on the marine trophic network has been well documented for OWFs in the Belgian part of the North Sea [100]. In this part of the North Sea, the uppermost subtidal meters of the turbine piles become densely populated by the blue mussel *Mytilus edulis*, a phenomenon called "*Mytilisation*" because of its predominance on constructions at sea [41,100]. Below the mussel zone, the biota is dominated by the amphipod *Jassa herdmani*, while the anemone *Metridium senile* is abundantly present on the lower parts of the piles. The density of the amphipod *Jassa herdmani* is known to exceed 1 million individuals per square meter. Along with the corophiid *Monocorophium acherusicum* (Costa, 1853), they form permanent epifauna, fouling the structures of the Belgian offshore wind farms [101]. This species and some caprellids, corophiids and stenothoids also make up very dense populations (>150,000 ind·m$^2$) on shipwrecks in the Belgian sector of the Southern Bight of the North Sea [102].

Wind turbines in Europe serve as foraging habitats for some fish species that feed on amphipods and decapods, such as Atlantic cod, pouting and the sculpin *Myoxocephalus scorpioides* (Fabricius, 1780) [42,103]; however, some pelagic species, such as horse mackerel *Trachurus trachurus*, occur in close proximity to the turbines and continue to prey predominantly on zooplankton [42].

In such new habitats, ref. [103] observed the aggregation and feeding behavior of the pouting *Trisopterus luscus* (Linnaeus, 1758), which was monitored in July-October 2009 at the Thornton Bank offshore wind farm in the Belgian sector of the North Sea. A large quantity of benthic prey was observed, including crustaceans and six amphipod species associated with a very large number of *Jassa hermani* (Walker, 1893), which is the dominant prey and which was present in more than 80% of the stomach contents of the pouting. Five other amphipods were also found in the stomachs: *Apolochus neapolitanus* (Della Valle, 1893), *Stenothoe marina* (Spence Bate, 1857), *Corophium* spp., *Phtisica marina* and *Megaluropus agilis*.

Ref. [104] hypothesized that *J. herdmani*, despite its small body size and simple filter apparatus, is a highly effective suspension feeder with a significant impact on neighboring communities of OWFs due to its high abundance. In a feeding experiment, ref. [104] indicated that *J. herdmani* alone is able to clear 0.33–4.71 km$^3$ of water per year in the southern North Sea. At the same time, these amphipods release 255–547 tonnes of carbon per year by defecation, thus enriching the surrounding soft sediments with organic matter. This study highlights that *J. hermani* could mediate the indirect effects of man-made structures in the North Sea, which could have a profound impact on pelagic and benthic habitats in OWF areas.

Refs. [41,42] analyzed the stable isotope signals (δ13C and δ15N) of the faunal communities associated with a wind turbine, as well as its SPL and the surrounding soft sediments; their results showed that the pelagic fish species *Trachurus trachurus* (Linnaeus, 1758) can be allocated to the *Jassa* zone since stomach content analysis revealed that this pelagic species mainly feeds on the amphipod *J. herdmani*. Ref. [42] also investigated the feeding ecology of fish species that abundantly occur near Belgian OWFs by examining the short- and long-term dietary composition of five species, combining stomach content and stable isotope analyses: the benthopelagic *Gadus morhua* Linnaeus, 1758, and *Trisopterus luscus*, the pelagic *Scomber scombrus* Linnaeus, 1758, and *Trachurus trachurus*, and the benthic *Myoxocephalus scorpioides* (Fabricius, 1780). *T. luscus*, young *G. morhua* and *S. scrombus* consumed the amphipod *Jassa herdmani* (87.6 ± 10.2%, 76.2 ± 19.3% and 61.2 ± 26.5% of the diet, respectively), while other amphipod species such as *Monocorophium acherusicum* (Costa, 1853), *Stenothoe valida* (Dana, 1852) and *Phtisica marina* were observed in smaller quantities.

The first offshore wind farm in North America was built on a pilot scale (five 6-MW turbines) approximately 5 km southeast of Block Island, Rhode Island, USA. The potential effects of this wind farm on dietary habits were examined for fish collected in a trawl survey conducted monthly over 7 years (October 2012 to September 2019) [105]. Stomach content analyses were carried out on Atlantic cod *Gadus morhua* Linnaeus, 1758, red hake *Urophycis chuss* (Walbaum, 1792), silver hake *Merluccius bilinearis* (Mitchill, 1814), spotted hake *Urophycis regia* (Walbaum, 1792), summer flounder *Paralichthys dentatus* (Linnaeus, 1766), winter flounder *Pseudopleuronectes americanus* (Walbaum, 1792), black sea bass *Centropristis striata* Linnaeus, 1758, haddock *Melanogrammus aeglefinus* Linnaeus, 1758, windowpane flounder *Scophthalmus aquosus* (Mitchill, 1815) and yellowtail flounder *Limanda ferruginea* (Storer, 1835) collected near the wind farm and in two reference areas during baseline, construction and operation periods. The diet composition of hake and flounder in all areas included a greater proportion of amphipods during the period of operation of the wind farm, but amphipods were found in the stomachs of all species (Appendix A).

## 8. Quantitative Relationships

The consumption of amphipods by each predator involves a benthic flux of matter and energy from the benthic prey to the predators.

Benthic amphipods are consumed by numerous predators, including fish, diving seabirds and other shorebirds. Demersal fish appear as opportunist predators, and amphipods are eaten as accessory or preferential prey. For example, [18] reported that ampeliscids are actively sought by capelin (e.g., 38 specimens of *Ampelisca sarsi* in a 7-cm *Trisopterus minutus* trawled on 15 September 1977) and rays (e.g., 47 individuals of *Ampelisca spinipes* in a 30-cm *Raja* trawled on 24 November 1977) on the fine sand community in the Bay of Morlaix.

In the Bering Sea, gray whale feeding provides a food source for surface-feeding birds [70]. These authors show that *Ampelisca* species were found in 100% of the stomachs of the black-legged kittiwake and the northern fulmar, with 57% in the thick-billed murre. *Byblis* species were found in 100% of the stomachs of the northern fulmar, 71% in the red phalarope, 57% in the thick-billed murre and only 14% in the black-legged kittiwake [70].

Ref. [85] estimated that a 6-m gray whale *Eschrichtius robustus* consumes 116 kg of wet weight in infaunal prey per 12-h day, while a 12-m whale consumes 552 kg per 12-h day in

Bamfield, British Columbia (Canada), largely including a dense aggregation of ampeliscid amphipods. The largest and densest known populations of the ampeliscid amphipod occur in the feeding area of gray whales on the northeastern shelf off Sakhalin Island, where *Ampelisca eschrichtii* is largely dominant [99]. In this area, *A. eschrichtii* populations are unlikely to be limited by the predation of western gray whales. These latter authors compared the energetics of gray whales and ampeliscids in the offshore Okhotsk Sea and the Chirikov Basin in the Bering Sea. The surface area occupied by the gray whale in the Chirikov Basin (4760 $km^2$) was more extensive than in the Okhotsk Sea (83 $km^2$), but the biomass of ampeliscids was greater in the Okhotsk Sea (338 $g{\cdot}m^{-2}$ wet weight) as against a 126 $g{\cdot}m^{-2}$ wet weight for the Chirikov Basin. The ampeliscid annual production in wet tonnes per whale was estimated at 1445 for the Okhotsk Sea and 211 for the Chirikov Basin.

To address the flux of matter, ref. [9] studied the suprabenthic fauna in the English Channel and considered positive transfers when the biomasses in the Benthic Boundary Layer (BBL) increased and negative transfers when the biomasses in the BBL decreased. Positive values correspond mainly to transfers from the benthos (for example, from amphipods) to the water column (including predation) and negative values to transfers in the opposite direction, i.e., the biomass is not consumed during pelagic migration. They estimated fluxes of living matter in mg $C{\cdot}m^{-2}$ per day in the Bay of Saint-Brieuc (the western part of the English Channel) during an annual cycle. At this site, the amphipod *Apherusa bispinosa* is dominant and forms a large part of the suprabenthic fauna. The mean daily transfer is estimated at 12.39 mg $C{\cdot}m^{-2}{\cdot}day^{-1}$ for an annual transfer of 4.52 $C{\cdot}m^{-2}{\cdot}y^{-1}$, with about 50% contributed by amphipods, but the predation rate remains unknown [9].

## 9. Conclusions

This review shows that benthic amphipods represent important prey—ranging from accessory to preferential prey—for marine vertebrates (birds, fish and mammals) and cephalopods. Most of the accessible data came from intertidal and shallow waters, while very few data are available for deeper zones.

Although predator and prey species are numerous and diverse (see Appendix A), some amphipods act as a major group, probably due to their ability to form very dense populations in excess of 10,000 $ind{\cdot}m^2$ and, in some cases, reaching 1 million individuals per $m^2$, such as *Jassa hermani* on hard shallow artificial habitats in the southern North Sea. The ampeliscids (*Ampelisca* and *Byblis* genera), corophiids (*C. volutator* and *Monocorophium acherusicum*), lysianassids (several species) and caprellids (*Caprella* spp. and *Phtisica marina*) appear among the main amphipod prey in many areas of the Worldwide Ocean (Appendix A).

Intertidal amphipods play a vital role for shorebirds at low tide and some juvenile fish at high tide. This is particularly the case for *Corophium volutator*, which lives in estuarine mudflat environments. The intense shorebird predation could interact with the *Corophium* population dynamics, i.e., leading to changes in the sex ratio, with males being more predated than the females, and a tendency toward semelparity, high resilience, etc.

Most demersal fish appear as opportunistic predators, nevertheless feeding on accessible prey that is made up of vagile epifauna—mainly decapods and peracarids—and among which the amphipods are actively predated. For shallow waters, there are no data supporting a link between intensive fish predation and amphipod population dynamics. Conversely, an important trophic cascade is illustrated with the high predation of the gray whale *Eschrichtius robustus* on dense Ampeliscidae populations in the North Pacific and Arctic Ocean. On some parts of the Pacific coast of North America (Baja California and Vancouver Island) and bordering the Arctic Ocean (the Bering, Chukchi and Beaufort seas), the abundance of amphipod populations is dramatically reduced due to the high predation of whales on dense *Ampelisca* and *Byblis* during their seasonal migration. As a hypothesis, it may be posited that the number of gray whales has diminished in the North American population due to the rarefaction of available prey. This illustrates the concept of the carrying capacity of an environment, which is defined as the maximum population size of a biological species that can be sustained by a specific environment, given the food and habitat. Nevertheless, gray whales mainly feed in the North Pacific and the Bering Sea, store up fat, and then migrate to Baja California to breed; they may feed occasionally during their migration and possibly on breeding groups poorer in prey. Ref. [106] estimated a lipid depletion of about 6% of the whale body weight per month during the migration, when the whales are presumed to fast.

Similarly, when benthic amphipods vanish from the seabed, such as during the first years after the Amoco Cadiz oil spill in Britany [18], the fish predator population suffers temporarily when the carrying capacity decreases due to the disappearance of *Ampelisca* productive populations.

To demonstrate the consumption of amphipods by higher-order predators, many methods have been employed, ranging from direct observations to molecular tools and from laboratory and field experiments to stomach content analysis. In spite of the difficulty of identifying the prey present in the stomach or digestive tract of predators, amphipods possess hard parts such as exoskeletons that resist digestion, which facilitates their identification based on only small morphological fragments such as appendages, antennae, telson, etc. However, this requires sufficient expertise to identify the prey at a species level. Nowadays, the use of DNA methods, and molecular tools in general, makes it possible to avoid carrying out the time-consuming analysis of stomach contents. Nevertheless, in most cases concerning the Amphipoda, the prey can be identified only at a high taxonomic level. In the future, molecular identification tools and the use of a systematic database could increase the precision of taxonomic determination; even if we could identify a particular amphipod species, it would still be impossible to count the number of predated individuals. In recent studies, both stomach contents and stable isotopes have been used to establish the food regime of predators; this combination of methods currently offers the best approach to investigating the prey/predator trophic food web.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Not applicable.

**Acknowledgments:** I thank Caen University and the Centre National de la Recherche Scientifique (UMR 6143 M2C CNRS) for welcoming me as at the M2C laboratory. I thank the *Journal of Marine Science and Engineering*, for his invitation to write this overview. I also thank Michael Carpenter for editing the English style and grammar of this paper and Kimy Wang for her help with the final edition of the typescript. I thank the three reviewers of the first version of the typescript for their very useful suggestions to improve the final version of this paper.

**Conflicts of Interest:** The author declares that he has no conflicts of interest.

## Appendix A. Predators and Amphipod Predated in the Worldwide Ocean

| Predators | Area | Benthic Amphipod Species | Reference |
|---|---|---|---|
| Birds | | | |
| Gentoo penguin *Pygoscelis papua* | Sub-Antarctic Crozet Islands | *Gondogeneia spinicoxa* | [2] |
| Imperial cormorant *Phalocrocorax atriceps* | Sub-Antarctic Crozet Islands | *Gondogeneia spinicoxa* | [2] |
| Salvin's prion *Pachyptila salvini* | Sub-Antarctic Crozet Islands | *Gondogeneia ushuaiae*, *Uristes murrayi* | [2] |
| Pintado petrel *Daption capensis* | Sub-Antarctic Crozet Islands | *Pontogeneiella brevicornis*, *Paracallisoma alberti*, *Parawaldeckia kidderi*, *Podocerus capillimanus*, Lysianassidae, Oedicerotidae | [2] |

| **Predators** | **Area** | **Benthic Amphipod Species** | **Reference** |
|---|---|---|---|
| Greatwinged petrel *Pterodroma macroptera* | Sub-Antarctic Crozet Islands | *Cyphocaris challengeri*, *Eurythenes obesus*, *E. gryllus* | [2] |
| Kerguelen petrel *Pterodroma brevirostris* | Sub-Antarctic Crozet Islands | *Cyphocaris richardi*, *Eurythenes obesus*, *E. gryllus*, *Paracallisoma alberti* | [2] |
| Blue petrel *Halobaena caerulea* | Sub-Antarctic Crozet Islands | *Cyphocaris richardi*, *Eurythenes obesus*, *E. gryllus*, *Paracallisoma alberti*, *Parandania boeki* | [2] |
| Lighmantled sooty albatross *Phoebetria palpebrata* | Sub-Antarctic Crozet Islands | *Eurythenes obesus* | [2] |
| Whitechinned petrel *Procellaria aequinoctialis* | Sub-Antarctic Crozet Islands | *Eurythenes obesus* | [2] |
| Softplumaged petrel *Pterodroma mollis* | Sub-Antarctic Crozet Islands | *Eurythenes obesus* | [2] |
| Blackbellied storm petrel *Fregetta tropica* | Sub-Antarctic Crozet Islands | *Eurythenes obesus* | [2] |
| Grayheaded albatross *Diomedea chrysostoma* | Sub-Antarctic Crozet Islands | *Eurythenes gryllus* | [2] |
| Sooty albatross *Phoebetria fusca* | Sub-Antarctic Crozet Islands | *Eurythenes gryllus* | [2] |
| Antarctic stern *Sterna vittata* | Southern Ocean | Benthic Gammaridea | [24] |
| Gentoo penguin *Pygoscelis papua* | Southern Ocean | Benthic Gammaridea | [24] |
| Emperor penguin *Aptenodytes forsteri* | Ross Sea, Antarctic Ocean | *Abyssorchomene rossi*, *A. plebs*, *Eusirus microps*, *Eusirus propeperdentatus*, *Uristes gigas* | [72] |
| Adelie penguin *Pygoscelis adeliae* | South Shetland Islands, Antarctic Ocean | *Eurymera monticulosa*, *Eusirus tridentatus*, *Cheirimedon femoratus*, *Hippomedon kergueleni* | [73] |
| Chinstrap penguin *Pygoscelis antarcticus* | South Shetland Islands, Antarctic Ocean | Gammaridae, *Eusirus tridentatus* | [73] |
| Gentoo penguin *Pygoscelis papua* | South Shetland Islands, Antarctic Ocean | Gammaridae, *Djerboa furcipes*, *Eurymera monticulosa*, *Eusirus propeperdentatus*, *E. tridentatus*, *Oradarea bidentata*, *Pontogeneiella brevicornis*, *Waldeckia obesa* | [73] |
| Briinnich's guillemots *Uria aalge* and *U. Zomvia* | Spitsbergen and Franz Josef Land | Amphipoda, *Gammarus*, *Gammarus wilkitskii* | [28] |
| Red phalarope *Phalaropus fulicarius* | Bering Sea, Northern Pacific | *Ampelisca*, *Byblis*, *Protomedia*, *Anonyx*, other Lysianassidae | [70] |
| Northern fulmar *Fulmarus glacialis* | Bering Sea, Northern Pacific | *Ampelisca*, *Byblis*, *Protomedia*, *Anonyx*, *Photis* | [70] |
| Brünnich's guillemot *Uria lomvia* | Bering Sea, Northern Pacific | *Ampelisca*, *Byblis*, *Protomedia*, *Anonyx*, *Photis*, Pleustidae | [70] |
| Black-legged kittiwake *Rissa tridactyla* | Bering Sea, Northern Pacific | *Ampelisca*, *Byblis*, *Pontoporia*, *Anonyx*, *Lembos* | [70] |
| Fulmar *Fulmarus glacialis* | Svalbard area, North Atlantic | *Anonyx nugax*, *Apherusa glacialis*, *Gammarellus homari*, *Gammarus wilkitzkii* | [71] |
| Black-legged kittiwake *Rissa tridactyla* | Svalbard area, North Atlantic | *Anonyx nugax*, *Apherusa glacialis*, *Gammarellus homari*, *Gammarus wilkitzkii* | [71] |
| Ivory gull *Pagophila eburnea* | Svalbard area, North Atlantic | *Anonyx nugax*, *Apherusa glacialis*, *Gammarellus homari*, *Gammarus wilkitzkii* | [71] |

| **Predators** | **Area** | **Benthic Amphipod Species** | **Reference** |
|---|---|---|---|
| Brünnich's guillemot *Uria lomvia* | Svalbard area, North Atlantic | *Anonyx nugax*, *Apherusa glacialis*, *Gammarellus homari*, *Gammarus wilkitzkii* | [71] |
| Black guillemot *Cepphus grille* | Svalbard area, North Atlantic | *Anonyx nugax*, *Apherusa glacialis*, *Gammarellus homari*, *Gammarus wilkitzkii* | [71] |
| Little auk *Alie alle* | Svalbard area, North Atlantic | *Anonyx nugax*, *Apherusa glacialis*, *Gammarellus homari*, *Gammarus wilkitzkii* | [71] |
| Redshank *Triga totanus* | Bristol Channel, Atlantic | *Corophium volutator* | [57,64] |
| Sandpiper *Calidris pusilla* | Bay of Fundy, Nova Scotia, Canada | *Corophium volutator* | [59] |
| Sandpiper *Calidris pusilla* | Bay of Fundy, Nova Scotia, Canada | *Corophium volutator* | [60] |
| Sandpiper *Calidris pusilla* | Bay of Fundy, Nova Scotia, Canada | *Corophium volutator* | [62] |
| Sandpiper *Calidris pusilla* | Bay of Fundy, Nova Scotia, Canada | *Corophium volutator* | [63] |
| Sandpiper *Calidris pusilla* | Bay of Fundy, New Brunswick, Canada | *Corophium volutator* | [48] |
| Varied thrushes *Ixoreus naevius* | Clallam County, Washington, Pacific | *Megalorchestia californiana*, *Traskorchestia traskiana* | [56] |
| Turnstone *Arenaria interpres* | North Wales, NE Atlantic | *Gammarus*, *Marinogammarus*, *Talitrus saltator* | [34] |
| Dunlin *Calidris alpina* | Eastern part of the English Channel, Atlantic | Gammaridea, *Bathyporeia* | [68] |
| Gray plover *Pluvialis squatarola* | Eastern part of the English Channel, Atlantic | *Gammaridea*, *Bathyporeia* | [68] |
| Sanderling *Calidris alba* | Eastern part of the English Channel, Atlantic | *Gammaridea*, *Bathyporeia* | [68] |
| Cephalopods | | | |
| Cuttlefish *Sepia officinalis* | Bay of Biscay, Morbiban Gulf, NE Atlantic | *Phtisica marina*, *Dexamine spinosa*, *Chaetogammarus marinus*, *Ampelisca brevicornis* | [31] |
| Cuttlefish *Sepia officinalis* | Bay of Biscay, NE Atlantic | Amphipoda, *Phtisica marina* | [107] |
| Cuttlefish *Sepia officinalis* | Southern Morocco, NE Atlantic | Amphipoda | [32] |
| Cuttlefish *Sepia officinalis* | Bay of Saint-Brieuc, English Channel | Amphipoda | [33] |
| Cuttlefish *Sepia officinalis* | Eastern part of the English Channel | Gammaridae, *Megaluropus agilis* | [74] |
| Fish | | | |
| Ray-finned fish *Gerlachea australis* | Southern Ocean | Benthic Gammaridea | [24] |
| Mawson's dragonfish *Cygnodraco mawsoni* | Southern Ocean | Benthic Gammaridea | [24] |
| Barbled plunderfish *Artedidraco mirus* | Southern Ocean | Benthic Gammaridea | [24] |
| Barbled plunderfish *Artedidraco orianae* | Southern Ocean | Benthic Gammaridea | [24] |
| Marbled plunderfish *Pogonophryne marmorata* | Southern Ocean | Benthic Gammaridea | [24] |

| **Predators** | **Area** | **Benthic Amphipod Species** | **Reference** |
|---|---|---|---|
| Magellan plunderfish *Harpagifer bispinis* | Southern Ocean | Benthic Gammaridea | [24] |
| Antarctic spiny plunderfish *Harpagifer antracticus* | Southern Ocean | Benthic Gammaridea | [24] |
| Humped rockcod *Gobionotothen gibberifrons* | Southern Ocean | Benthic Gammaridea | [24] |
| Antarctic yellowbelly rockcod *Nothothenia coriiceps* | Southern Ocean | Benthic Gammaridea | [24] |
| Cod icefish *Lepidonothen nudifrons* | Southern Ocean | Benthic Gammaridea | [24] |
| Pink cusk-eel *Genypterus blacodes* | South Atlantic, Argentina coast | Gammaridae, Caprellidae, *Ampelisca* | [30] |
| Shiner perch *Cymatogaster aggregata* | Padilla Bay, Washington, USA | Caprellidae *Caprella laeviuscula* | [80] |
| Black croaker *Atrobucca nibe* | Southern coastal waters of Zhejiang, China | Gammaridea, *Ampelisca*, *Monoculodes* | [45] |
| Gurnard *Trigla lineata* | Off Plymouth, English Channel | Amphipoda | [16] |
| Common dragonet *Callionymus lyra* | Off Plymouth, English Channel | Amphipoda | [16] |
| Young plaice *Pleuronectes platessa* | Off Plymouth, English Channel | Amphipoda | [16] |
| Ray *Raja clavata* | Off Plymouth, English Channel | Amphipoda, *Ampelisca* | [16] |
| Ray *Raja maculata* | Off Plymouth, English Channel | Amphipoda, *Ampelisca* | [16] |
| Ray *Raja* spp. | Bay of Morlaix, English Channel | Gammaridea, *Ampelisca*, *Ampelisca spinipes*, *Bathyporeia* | [18] |
| Whiting *Merlangius merlangus* | Bay of Morlaix, English Channel | Gammaridea, *Ampelisca*, *Bathyporeia* | [18] |
| Pouting *Trisopterus luscus* | Bay of Morlaix, English Channel | Gammaridea, *Ampelisca* | [18] |
| Poor cod *Trisopterus minutus* | Bay of Morlaix, English Channel | Gammaridae, *Ampelisca*, *Ampelisca sarsi*, *Bathyporeia elegans*, *Apherusa* | [18] |
| Surmullet *Mullus surmuletus* | Bay of Morlaix, English Channel | Gammaridea, *Ampelisca*, *Bathyporeia* | [18] |
| Lesser weever *Echiichthys vipera* | Bay of Morlaix, English Channel | Gammaridea, *Bathyporeia* | [18] |
| Gobies *Pomatoschistus* | Bay of Morlaix, English Channel | Gammaridea, *Ampelisca* | [18] |
| Common dragonet *Callionymus lyra* | Bay of Morlaix, English Channel | Gammaridea, *Ampelisca*, *Bathyporeia* | [18] |
| European plaice *Pleuronectes platessa* | Bay of Morlaix, English Channel | Gammaridea | [18] |
| Dover sole *Solea vulgaris* | Bay of Morlaix, English Channel | Gammaridea, *Ampelisca*, *Ampelisca sarsi*, *Bathyporeia* | [18] |
| Mediterranean scaldfish *Arnoglossus laterna* | Bay of Saint-Brieuc, English Channel | Amphipoda | [33] |
| Solenette *Buglossidium luteum* | Bay of Saint-Brieuc, English Channel | Amphipoda | [33] |

| **Predators** | **Area** | **Benthic Amphipod Species** | **Reference** |
|---|---|---|---|
| Common dragonet *Callionymus lyra* | Bay of Saint-Brieuc, English Channel | Amphipoda | [33] |
| Black goby *Gobius niger* | Bay of Saint-Brieuc, English Channel | Amphipoda | [33] |
| Surmullet *Mullus surmuletus* | Bay of Saint-Brieuc, English Channel | Amphipoda | [33] |
| Black sea bream *Spondyliosoma cantharus* | Bay of Saint-Brieuc, English Channel | Amphipoda | [33] |
| European flounder *Platichthys flesus* | Bay of Seine, English Channel | *Cherirocratus sundewalli*, *Pariambus typicus* | [78] |
| Poor cod *Trisopterus minutus* | Bay of Seine, English Channel | Gammaridea | [78] |
| Ray *Raja clavata* | Bay of Seine, English Channel | Gammaridea, *Pariambus typicus* | [78] |
| Dover sole *Solea vulgaris* | Bay of Seine, English Channel | Gammaridea | [78] |
| Lesser weever *Echiichthys vipera* | Bay of Seine, English Channel | Gammaridea | [78] |
| Pogge *Agonus cataphractus* | Bay of Seine, English Channel | Gammaridea | [78] |
| Solenette *Buglossidium luteum* | Bay of Seine, English Channel | Gammaridea, *Abdulomelita obtusata*, *Ampelisca brevicornis*, *A. spinipes*, *A. tenuicornis*, *Bathyporeia*, *Corophium volutator*, *Leucothoe incisa*, *Megaluropus agilis*, *Melita palmata*, *Moncoculodes*, *Orchomenella nana*, *Perioculodes longimanus*, *Pontocrates altamarinus*, *Urothoe elegans* | [79] |
| Plaice *Pleuronectes platessa* | Bay of Seine, English Channel | Gammaridea, *Ampelisca brevicornis*, *Pontocrates altamarinus* | [79] |
| Dover sole *Solea vulgaris* | Bay of Seine, English Channel | *Ampelisca brevicornis*, *A. spinipes*, *Corophium volutator*, Ischyroceridae, *Megaluropus agilis*, *Monoculodes*, *Orchomenella nana*, *Perioculodes longimanus* | [79] |
| Ray *Raja clavata* | Eastern part of the English Channel | Gammaridae, *Megaluropus agilis* | [74] |
| Whiting *Merlangius merlangus* | Eastern part of the English Channel | Gammaridae, *Megaluropus agilis* | [74] |
| Lesser weever *Echiichthys vipera* | Eastern part of the English Channel | Gammaridae, *Apherusa bispinosa* | [74] |
| Common dragonet *Callionymus lyra* | Eastern part of the English Channel | Gammaridae, *Apherusa bispinosa* | [74] |
| Plaice *Pleuronectes platessa* | Eastern part of the English Channel | Gammaridae, *Megaluropus agilis* | [74] |
| Common dab *Limanda limanda* | Eastern part of the English Channel | Gammaridae, *Megaluropus agilis* | [74] |
| Dover sole *Solea vulgaris* | Eastern part of the English Channel | Gammaridae, *Apherusa bispinosa* | [74] |
| Solenette *Buglossidium luteum* | Eastern part of the English Channel | Gammaridae, *Megaluropus agilis* | [74] |
| Mediterranean scaldfish *Arnoglossus laterna* | Eastern part of the English Channel | Gammaridae, *Apherusa bispinosa*, *Megaluropus agilis* | [74] |

| **Predators** | **Area** | **Benthic Amphipod Species** | **Reference** |
|---|---|---|---|
| Pogge *Agonus cataphractus* | Eastern part of the English Channel | Gammaridae, *Megaluropus agilis* | [74] |
| Pouting *Trisopterus luscus* | Thorntonbank, Belgian part of the North Sea | *Jassa hermani*, *Apolochus neapolitanus*, *Stenothoe marina*, *Corophium*, *Phtisica marina*, *Megaluropus agilis* | [103] |
| Cod *Gadus morhua* | Wind farms, Belgian part of the North Sea | *Jassa herdmani*, *Monocorophium acherusicum*, *Phtisica marina*, *Stenothoe valida* | [42] |
| Pouting *Trisopterus luscus* | Wind farms, Belgian part of the North Sea | Amphipoda, *Jassa herdmani*, *Monocorophium acherusicum*, *Phtisica marina*, *Stenothoe valida* | [42] |
| *Atlantic horse mackerel Trachurus trachurus* | Wind farms, Belgian part of the North Sea | *Jassa herdmani*, *Monocorophium acherusicum* | [42] |
| Flounder *Pseudopleuronectes americanus* | North Bay of Fundy, Canada | *Corophium volutator* | [76] |
| Ray *Leucoraja ocellata* | North Bay of Fundy, Canada | *Corophium volutator* | [76] |
| Alaska skate *Bathyraja parmifera* | Kuril Islands and Kamchatka, North Pacific | Amphipoda | [81] |
| Alaska skate *Bathyraja matsubarai* | Kuril Islands and Kamchatka, North Pacific | Amphipoda | [81] |
| Aleurian skate *Bathyraja aleutica* | Kuril Islands and Kamchatka, North Pacific | Amphipoda | [81] |
| White blotched skate *Bathyraja maculata* | Kuril Islands and Kamchatka, North Pacific | Amphipoda | [81] |
| Sandpaper skate *Bathyraja interrupta* | Kuril Islands and Kamchatka, North Pacific | Amphipoda | [81] |
| Okkotsk skate *Bathyraja violacea* | Kuril Islands and Kamchatka, North Pacific | Amphipoda | [81] |
| Brown skate *Bathyraja minispinosa* | Kuril Islands and Kamchatka, North Pacific | Amphipoda | [81] |
| Ray *Raja brachyura* | Bay of Douarnenez, Northeastern Atlantic | Amphipoda, *Kroyera carinata* | [22] |
| Ray *Raja clavata* | Bay of Douarnenez, Northeastern Atlantic | Amphipoda | [22] |
| Ray *Raja montagui* | Bay of Douarnenez, Northeastern Atlantic | Amphipoda, *Ampelisca brevicornis*, *A. spinipes*, *Bathyporeia pelagica*, *Kroyera carinata* | [22] |
| *Boarfish Capros aper* | Offshore Arcahon, Bay of Biscay, Atlantic | Gammaridea | [19] |
| Surmullet *Mullus surmuletus* | Offshore Arcahon, Bay of Biscay, Atlantic | Gammaridea, *Kroyera carinata* | [19] |
| Longfin gurnard *Chelidonichthys obscurus* | Offshore Arcahon, Bay of Biscay, Atlantic | Gammaridea, *Westwoodilia caecula* | [19] |
| Dover sole *Solea vulgaris* | Offshore Arcahon, Bay of Biscay, Atlantic | Gammaridea, *Hippomedon denticulatus*, *Ampelisca brevicornis* | [19] |
| Sand sole *Pegusa lascaris* | Offshore Arcahon, Bay of Biscay, Atlantic | Gammaridea, *Hippomedon denticulatus*, *Ampelisca brevicornis* | [19] |

| Predators | Area | Benthic Amphipod Species | Reference |
|---|---|---|---|
| Wedge sole *Dicologlossa cuneata* | Offshore Arcahon, Bay of Biscay, Atlantic | Gammaridea, *Hippomedon denticulatus*, *Ampelisca brevicornis* | [19] |
| Atlantic cod *Gadus morhua* | Northwestern Atlantic, shallow Southeast Shoal | *Anonyx sarsi*, *Psammonyx terranovae*, *Hippomedon serratus*, *Monoculodes edwardsi*, *M. tuberculatus*, *M. intermedius*, *Unciola irrorata*, *Amphiporeia lawrenciana*, *Acathohaustorius spinosus*, *Pontogeneia inermis*, *Metopa alderi*, *Ischyrocerus anguipes*, *Corophium bonelli*, *Paramphithoe hystrix*, *Pardalisca cuspidatus*, *Tiron acanthurus*, *Caprella septentrionalis*, *Aeginina longicornis* | [82] |
| Atlantic cod *Gadus morhua* | Northwestern Atlantic, sympagic ice associated | *Pseudalibrotus nanseni*, *Gammarus wilkitzkii*, *Pseudalibrotus glacialis*, *Gammaracanthus loricatus* | [82] |
| Atlantic cod *Gadus morhua* | Northwestern Atlantic, Grand Bank | *Anonyx nugax*, *A. laticoxae*, *A. lilljeborgi*, *Eusirus cuspidatus*, *Rozinante fragilis*, *Unciola leucopis*, *Onisimus edwardsi*, *Haploops tubicola*, *Arrhis phylloyx*, *Paroediceros lynceus*, *Melita dentata*, *Ischyrocerus commensalis* | [82] |
| Atlantic cod *Gadus morhua* | Northwestern Atlantic, Cold Intermediate Layer | *Anonyx makarovi* | [82] |
| Atlantic cod *Gadus morhua* | Northwestern Atlantic, Continental Slope | *Anonyx nugax*, *A. ochoticus*, *A. compactus*, *Tmetonyx cicada*, *Haploops setosa*, *Stenopleustes latipes*, *Eusirus holmi*, *Maera loveni*, *Goesia depressa*, *Ischyrocerus megacheir*, *Orchomene serratus*, *Uristes umbonatus*, *Aristias tumidus*, *Stegocephalus inflatus*, *Haliragoides inermis*, *Eurysteus melanops*, *Lilljeborgia fissicornis*, *Protomedeia stephenseni*, *Neohela monstrosa*, *Ischyrocerus latipes* | [82] |
| Atlantic cod *Gadus morhua* | Northwestern Atlantic, all depths | *Ampelisca eschrichti*, *A. macrocephala*, *Byblis gaimardi*, *Erichthonius hunteri*, *Tmetonyx albidus*, *Syrrhoe crenulatus*, *Rhachotropis aculeata* | [82] |
| Flounder *Pseudopleuronectes americanus* | Starrs Point, NE of the Bay of Fundy, Canada | *Corophium volutator* | [76,83] |
| Ray *Leucoraja ocellata* | Starrs Point, NE of the Bay of Fundy, Canada | *Corophium volutator* | [76,83] |
| Atlantic cod *Gadus morhua* | Block Island, Rhode Island, Atlantic | Gammaridae, Ampeliscidae, Aoridae, Melitidae, *Caprella penantis*, *Unciola* | [105] |
| Red hake *Urophycis chuss* | Block Island, Rhode Island, Atlantic | Gammaridae, Ampeliscidae, Aoridae, Melitidae, *Caprella penantis*, *Unciola* | [105] |
| Silver hake *Merluccius bilinearis* | Block Island, Rhode Island, Atlantic | Ampeliscidae, Aoridae, Gammaridae, Pleustidae, *Unciola* | [105] |
| Spotted hake *Urophycis regia* | Block Island, Rhode Island, Atlantic | Amphipoda, Ampeliscidae, Aoridae, Gammaridae, Pleustidae, Lysianassidae, *Caprella penantis*, *Unciola* | [105] |

| **Predators** | **Area** | **Benthic Amphipod Species** | **Reference** |
|---|---|---|---|
| Summer flounder *Paralichthys dentatus* | Block Island, Rhode Island, Atlantic | Amphipoda, Ampeliscidae, Aoridae, Gammaridae, Melitidae, Pleustidae, *Unciola* | [105] |
| Winter flounder *Pseudopleuronectes americanus* | Block Island, Rhode Island, Atlantic | Gammaridae, Lysianassidae, Melitidae, Oridae, Photidae, Pleustidae, *Calliopus laeviusculus*, *Caprella penantis*, *Listriella*, Unciola | [105] |
| Black sea bass *Centropristis striata* | Block Island, Rhode Island, Atlantic | Ampeliscidae, Aoridae, Gammaridae, *Unciola* | [105] |
| Haddock Melanogrammus aeglefinus | Block Island, Rhode Island, Atlantic | Ampeliscidae, Gammaridae | [105] |
| Windowpane flounder *Scophthalmus aquosus* | Block Island, Rhode Island, Atlantic | Gammaridae | [105] |
| Yellowtail flounder *Limanda ferruginea* | Block Island, Rhode Island, Atlantic | Ampeliscidae, Gammaridae | [105] |
| Labrid fish *Coris julis* | Sardinia, Mediterranean Sea | *Aora spinicornis*, *Phtisica marina*, *Apherusa chiereghinii* | [51] |
| Black croaker *Atrobucca nibe* | Southern coastal waters of Zhejiang, China | Gammaridea, *Ampelisca*, *Monoculodes* | [45] |
| Mammals | | | |
| Walruses *Odobenus rosmarus* | Bering Sea, North Pacific | Amphipoda, Ampeliscidae | [86] |
| Gray whale *Eschrichtius robustus* | North Pacific | Ampeliscidae, *Ampelisca*, *Byblis* | [86,90] |
| Gray whale *Eschrichtius robustus* | Bering and Chukchi Seas, Pacific | *Pontoporeia femorata*, *P. affinis*, *Anonyx nugax*, *Ampelisca macrocephala*, *A. eschrichtii*, *Nototropis brueggeni*, *N. ekmani* | [94,96] |
| Gray whale *Eschrichtius robustus* | Vancouver Island, North Pacific | *Ampelisca*, *Atylus borealis* | [37] |
| Gray whale *Eschrichtius robustus* | Vancouver Island, North Pacific | *Ampelisca agassizi*, *A. careyi* | [95] |
| Gray whale *Eschrichtius robustus* | Kamchatka North Pacific Ocean | *Ampelisca eschrichtii* | [98] |

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