

Trophodynamics in a Shallow Lagoon off Northwestern Europe (Culbin Sands, Moray Firth): Spatial and Temporal Variability of Epibenthic Communities, Their Diets, and Consumption Efficiency

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Vanda Mariyam Mendonça, David George Raffaelli, Peter R. Boyle, and Chas Emes (2009) Trophodynamics in a shallow lagoon off northwestern Europe (Culbin Sands, Moray Firth): Spatial and temporal variability of epibenthic communities, their diets, and consumption efficiency. *Zoological Studies* 48(2): 196-214. Epibenthic communities and their diets, at Culbin Sands (a cold-temperate coastal lagoon in the Moray Firth, northeastern Scotland), were sampled every 2-4 wks for 3 yrs (1994-1996). These communities were more abundant and diverse in warmer months, especially in less-exposed areas of the lagoon. The most common species were the brown shrimp *Crangon crangon*, the shore crab *Carcinus maenas*, and teleost fish (sandeel *Ammodytes tobianus*, sticklebacks *Gasterosteus aculeatus* and *Spinachia spinachia*, seascorpion *Myoxocephalus scorpius*, gobies *Pomatoschistus microps* and *Pomatoschistus minutus*, flounder *Platichthys flesus*, and plaice *Pleuronectes platessa*). Diets of these epibenthic predators included benthic infauna (especially polychaetes *Eteone longa*, *Pygospio elegans*, and *Fabricia sabella*; oligochaetes *Tubificoides benedini*; isopods *Eurydice pulchra*; and bivalves *Cerastoderma edule* and *Macoma balthica*), small epibenthic organisms (amphipods especially *Bathyporeia pilosa* and *Gammarus* sp., and juvenile crabs *Carcinus maenas* and shrimp *Crangon crangon*), and zooplankton (harpacticoids, ostracods mostly *Cypris* sp., calanoid copepods, mysids *Praunus flexuosus*, and fish eggs and larvae). Insect larvae (Chironomidae) were also common in the stomach contents of the epibenthic predators. In fact, prey items with higher indices of relative importance for the most abundant predators (brown shrimp, common gobies, and plaice) were insect larvae for shrimp, amphipods *Bathyporeia pilosa* for shrimp and gobies, harpacticoids for plaice and gobies, and bivalves (larvae and siphons of adult individuals) mostly for plaice. Brown shrimp, common goby, and plaice had daily consumption levels of 1%, 3%, and 2.5% of their own body wet weights, respectively. Energy flows of 150, 68, and 65 kJ m⁻² yr⁻¹ were estimated from benthic invertebrates to brown shrimp, common gobies, and plaice, equivalent to consumption efficiencies of 30%, 15%, and 15%, respectively, of the standing stock of benthic invertebrates and small epibenthic species such as amphipods. <http://zoolstud.sinica.edu.tw/Journals/48.2/196.pdf>

Key words: Consumption efficiency, Culbin Sands, Epibenthic predators, Moray Firth, Relative importance of prey.

Coastal ecosystems host complex benthic communities, supporting a wide range of epibenthic predators, some of which use the shallow, warm, nutrient-rich waters as nursery and overwintering areas (Hostens and Mees 2003, ICES 2005).

Abiotic factors may lay behind migrations of these species, so that to avoid colder waters, they move to warmer areas. Nevertheless, biotic relationships also induce migration patterns, as epibenthic species may move to avoid predators, but also in

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search of their own prey (Oh et al. 2001, Oh and Hartnoll 2004).

Epibenthic predators mainly feed on adult benthic invertebrates (e.g., polychaetes, oligochaetes, and bivalves), zooplanktonic crustaceans (e.g., harpacticoids, ostracods, and copepods), and eggs and juvenile stages of epibenthic (or benthopelagic) and pelagic species (Nakaya et al. 2004). A study by Pihl (1985) in northwestern (NW) European waters (Sweden) showed that benthic macrofauna comprised 70% in volume of the total stomach contents of epibenthic species. The remaining consisted of meiofauna, small epibenthic fauna (such as amphipods), and particulate matter. Of the meiofauna, zooplankton was frequently eaten by smaller epibenthic predators. Larger fish species consumed bivalves, polychaetes, and crustaceans.

The abundance, biomass, and production of the most common epibenthic predators of shallow waters in the North Sea and generally in NW European waters are generally high (ICES 2006). Similar results are also available for San Francisco Bay, CA, USA (Wahle 1985) and Japan (Nakaya et al. 2004). According to Evans (1983), in Gullmar Fjord (Sweden) in the North Sea, in the late 1970s and early 1980s, production ranged 0.6-2.4 g dry weight (DW) $m^{-2} yr^{-1}$ for brown shrimp *Crangon crangon* (with two main spawning periods, one in Apr.-May and another in Oct.); 0.1-0.2 g (DW) $m^{-2} yr^{-1}$ for the sand goby *Pomatoschistus minutus* (which spawns in summer), and 0.2-0.3 g (DW) $m^{-2} yr^{-1}$ for plaice *Pleuronectes platessa* (which also spawns in summer). In fact, in the northeast (NE) Atlantic, zooplankton is abundant throughout the year, with spring and autumn bloom periods, providing better conditions for their predators during warmer months (Edwards et al. 2006).

Other studies also carried out in Sweden (Pihl 1985) in 3 areas lacking vegetation (exposed, semi-exposed, and sheltered) and a 4th with vegetation, had annual production values for epibenthic fauna (brown shrimp *Crangon crangon*, common goby *Pomatoschistus microps*, sand goby *P. minutus*, plaice *Pleuronectes platessa*, and the shore crab *Carcinus maenas*) of up to 6 g ash-free dry weight (AFDW) $m^{-2} yr^{-1}$, corresponding to up to 100 individuals (ind.) m^{-2} for these species combined. In the same area, these predators consumed up to 98% of the annual production of the amphipod *Corophium volutator*, 92% of the cockle *Cerastoderma edule*, and 62% of the clam *Mya arenaria*. In some shallow waters off NE Scotland outside the Moray Firth, in the Ythan

estuary, densities of these predators combined were >100 ind./ m^2 (Raffaelli et al. 1989), with fish taking 54% of the deposit-feeder production (Baird and Milne 1981), corresponding to a consumption by epibenthic predators higher than that recorded in many other aquatic ecosystems.

In fact, some epibenthic predators such as the brown shrimp *Crangon crangon* are considered highly significant regulators of other epibenthic carnivores in shallow waters in the Wadden Sea, where they may predate 20%-35% of the benthic production (including planktonic stages), as well as eggs and planktonic stages of many fish species (Taylor and Collie 2003). On the other hand, part of the annual production of shrimp in shallow waters is also cropped by small-sized epibenthic predators, providing a negative feedback which tends to stabilize the system. In fact, diets of epibenthic predator populations may vary as a result of adaptations to their habitat conditions, but also as a result of adaptive foraging in intraguild predation systems (Krivan 2000, Okuyama and Ruyle 2003).

In the present study, we studied the epibenthic communities at Culbin Sands lagoon, Moray Firth, NE Scotland, by analyzing their spatial variations within the lagoon throughout the year, their diets, and consumption efficiencies.

MATERIALS AND METHODS

Study area

The Moray Firth and adjacent coasts experience a mild maritime climate due to the prevailing southwesterly winds and the warming influence of the North Atlantic Current. At sea level, the mean air temperature varies from a minimum of about 6°C in Mar. to a maximum of 12.5-13°C in July and Aug. (UKDMAP 1998). The salinity of the waters close to the coast fluctuates more than those in the outer Moray Firth, because of tidal currents mixing and the influence of river inputs.

The standing stock of phytoplankton in the Moray Firth peaks in Mar.-Apr. and again in Aug.-Sept. (Adams and Martin 1986, Heath et al. 1989, DTI 2004). Common phytoplankton species are *Rhizosolenia shrubsolei*, *Stephanopyxis turris*, *Lauderia borealis*, *Cerathium* spp., and *Peredinium* spp. Zooplankton communities are dominated by copepods including *Centropages hamatus*, *Temora longicornis*, *Acartia clausi*, *Pseudocalanus*

elongatus, *Calanus helgolandicus*, and *Calanus finmarchicus*. Copepod abundance reaches a peak in May following a phytoplankton bloom and remains high throughout the summer before declining sharply between Sept. and Nov.

The Moray Firth, NE Scotland, has been designated a Special Area of Conservation (SAC) for a number of species including cetaceans, and in a relatively recent assessment by the World Wildlife Fund (Gubbay 2006), its suitability of becoming a Marine Protected Area (MPA) or perhaps a Marine Biosphere Reserve (a concept promoted by UNESCO) was discussed. However, the report also pointed out a general lack of extensive detailed scientific studies on the ecology of both benthic and pelagic biodiversity in the Moray Firth, and considered the existing knowledge scarce or limited to certain species (e.g., cetaceans) when compared with other areas in the northeast Atlantic such as the Irish Sea or the German Bight.

Culbin Sands Nature Reserve, on the southern shores of the Moray Firth, includes a terrestrial (planted) forest of 28 ha, and a bare sand dune enclosing a lagoon with 1.5 ha of intertidal flats. The lagoon has a permanently submerged gully with a maximum depth of 2.5 m at high tide, and closer to the mouth of the main gully, the sediment is coarser and poorer in silt (Mendonça 1997). There are no inputs from rivers, but the salinity fluctuates around 34‰, with lower values at low tide due to fresh water seeping in through the sand (Adams and Martin 1986). Behind the bar, seagrass beds of *Zostera noltii* and *Z. marina* have been identified (Greathead et al. 2006). In the Culbin Sands area, the salt marsh covers 60.28 ha, with the common salt marsh grass *Puccinellia maritima* as the dominant species, but *Salicornia* spp., *Pevetia canaliculata*, *Spartina* spp., and the Scottish curvy grass *Cochleria scotica* (which occurs on the upper edge of the salt marsh) are also found. Although the salt marsh is an uncommon feature of NE Scotland, the salt marsh of Culbin Sands and that of the adjacent Findhorn estuary comprise 70% of the region's salt marsh (Greathead et al. 2006).

Culbin Sands Nature Reserve has been relatively isolated from human disturbance since the 19th century, following the exodus of human populations from the area, when the unstable characteristics of its sand dune became hazardous for local settlements. Apart from the intervention through the planting of a stabilizing forest, and poles erected on the tidal flats during World War II

(as glider defense to prevent the landing of unwanted enemy vessels), the area has not been subjected to other anthropogenic impacts, for at least a century. The isolation of the area for this long has provided an opportunity for wildlife populations to prosper in a relatively undisturbed environment, currently becoming a site of interest also for its biodiversity, in both its aquatic and terrestrial habitats. Culbin Sands is now a Special Site of Scientific Interest (SSSI), a RAMSAR Site, and a Special Area of Conservation/Special Protection Area (SAC/SPA) under the Habitats Directive 1992.

The published scientific literature on Culbin Sands mostly concerns its geology (Smith 1986), and information on the ecology of this aquatic ecosystem was scarce until we initiated our 3-yr-study (1994-1996). The benthic infauna (Mendonça et al. 2008) and impacts of overwintering teleost fish (Mendonça et al. 2007a) and shorebirds (Mendonça et al. 2007b) on benthic invertebrates were recently described as a part of our extensive studies. Herein, we specifically detail the ecology of the epibenthic communities.

Spatial and temporal variability of epibenthic predators

In order to study epibenthic communities at Culbin Sands lagoon, 3 sites were surveyed. Site 1 was located in a less-exposed area where most of the mussel beds of *Mytilus edulis* were concentrated; site 2 was closer to the bar; and site 3 was not as exposed as site 2 and not as sheltered as site 1 (Fig. 1). Median particle sizes of sediments were up to 120 μm at sites 1 and 3, and 130 μm -140 μm at site 2; silt contents were 0% - 5% at the 3 sites (Mendonça 1997).

Epibenthic species were sampled during the ebb tide, at depths of 0.5-1 m, from May 1994 to Aug. 1996. Sampling was conducted every 2-4 wks (once a month in winter; and every 2 wks from spring to autumn when variations are more likely to occur), using a push-net (with a 2 m long handler and a 1.5 m long bag (of 1 mm mesh), with a metal-frame entrance of 0.5 x 0.5 m in area) pushed by hand for about 15 min at a time along a transect (of 50 m in length) in the main gully. As the efficiency of the net was unknown, the abundance of epibenthic species was estimated on a logarithmic scale (0-1, 1-10, and 10-100 ind./m²) based on the densities caught in the nets.

All specimens caught in the nets were preserved *in situ* in 10% formalin, in order to

immediately stop digestion, for later stomach content identification. Back in the laboratory, specimens were identified using Hayward and Ryland (1990), weighed wet (WW), and measured to the nearest millimeter (from the eyes to the telson for shrimps, carapace width for crabs, and from the snout to the tail for fish). Multivariate analyses (KCS 2001) were used to investigate the characteristics of these epibenthic communities as follows: Spatial variations were analyzed by a

detrended correspondence analysis (DECORANA); temporal variations were analyzed by principal component analyses (PCAs); and species diversity at the three sites was analyzed by the Shannon diversity index: $H = -(\sum p_i \ln p_i)$, where i ranges from 1 to s , with s being the total number of species in the community (or richness), and for each species, the proportion of individuals or biomass that contributes to the total of a sample is p_i for the i^{th} species.

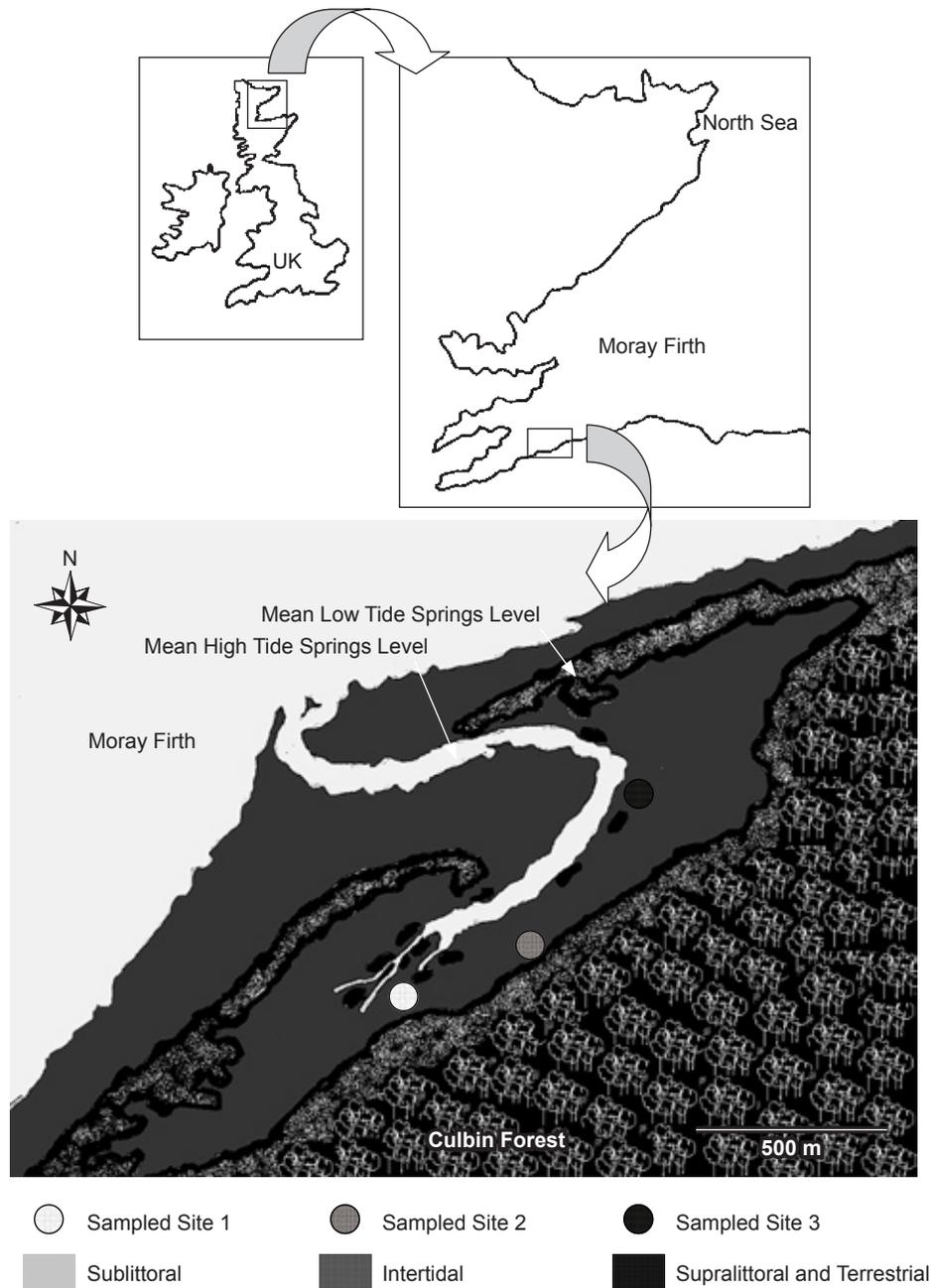


Fig. 1. The 3 sampled sites (1-3) at Culbin Sands lagoon, Moray Firth, NE Scotland. Dark patches near the main gully correspond to mussel beds of *Mytilus edulis*.

Diets of epibenthic predators and indices of relative importance of their prey

Gut contents of all sampled epibenthic predators were examined under a dissecting microscope, and prey items were identified (to species or otherwise lowest taxon level) using Hayward and Ryland (1990). Prey items were counted, and the respective relative volume in the predator stomach (volumetric composition, %) was registered. There are several ways to test the relative volume, one of which uses a test-tube with water. Sand grains were generally found in the stomachs of shrimp and in smaller proportions in gobies, but were not taken into account in the volume calculations. Diets of the crab *Carcinus maenas* were not quantified because of the fragmentary nature of the ingested prey remains, which did not allow quantification either of the number or volume of prey. Due to the small sample size (only one individual during the 3-yr-study), the stomach contents of the starfish *Asteria rubens* (a species known to feed on bivalves, Cameron and Mitchell 1999), and pipefish *Nerophis lumbriciformis* (known to feed on small zooplanktonic crustaceans, Lyons and Dunne 2004), were not analyzed in the present study. Finally, stomach contents of other species also caught in the nets, such as the zooplanktonic mysids *Praunus flexuosus* (known to feed on zooplanktonic crustaceans, Boscarino et al. 2007) and the intertidal and subtidal amphipods *Bathyporeia pilosa* (benthic grazers, Herman et al. 2000) were also not analyzed. The diets of all analyzed epibenthic predators were compared using cluster analyses and DECORANA (KCS 2001).

The diets (volumetric composition) of the most common predator species (brown shrimp *Crangon crangon*, common goby *Pomatoschistus microps* and plaice *Pleuronectes platessa*) were further compared over time and between sites by ANOVA, after arc-sin transformation of the data to achieve normality. Tukey's pairwise comparisons were conducted when the probability (*P*) level was significant. The *P* level of significance was decided after Bonferroni sequential tests (Sokal and Rohlf 1995). Sample sizes were *n* = 15 ind. of *Crangon crangon* per size class (< 20 and 20-50 mm) per site and per month; *n* = 10 ind. of *Pomatoschistus microps* per site and per month (no size classes were considered as they were mostly about the same size), and *n* = 15 ind. of *Pleuronectes platessa* per size class (< 20, 20-50, and > 50 mm)

per site and per month. Diets of common gobies *Pomatoschistus microps* were compared with those of sand gobies *Pomatoschistus minutus* (*n* = 15 ind. per species, pooled over all sites and time, after which no significant differences over site or time for each species were recorded).

For the most abundant epibenthic predators, (brown shrimp *Crangon crangon*, common goby *Pomatoschistus microps*, and plaice *Pleuronectes platessa*), the numerical composition (NC) index, the volumetric composition (VC) index, the frequency of occurrence (FO) index, and the index of relative importance (IRI), were estimated as follows: NC (%) = (number of prey item *i* / total number of prey in the stomach) x 100 (Ikusemiju and Olaniyan 1977); VC (%) = (volume of prey item *i* / total volume in the stomach) x 100 (Larimore 1957); FO (%) = (number of stomachs with prey item *i* / total number of stomachs) x 100 (Dinnen 1951); and IRI = (NC + VC) x FO (Prince 1975). For these estimates, sample sizes were *n* = 30 ind. of *Crangon crangon* (30-40 mm); *n* = 30 ind. of *Pomatoschistus microps* (20-30 mm); and *n* = 30 ind. of *Pleuronectes platessa* (30-50 mm). For all species, samples were pooled over time and sites, after previous analyses proved that there were no significant differences in diets of these predators over time or sites.

Consumption efficiency of epibenthic predators

For the most common epibenthic species (brown shrimp *Crangon crangon*, common goby *Pomatoschistus microps*, and plaice *Pleuronectes platessa*), daily consumption was estimated as a percentage of the predator body weight as follows: Daily ingestion rate (%) = weight of stomach content (g WW) / body weight (g WW) x 100 x 2 tidal cycles per day. Sand grains in the stomach were not taken into account when estimating daily ingestion rates. Stomach contents of these predators were observed in every tide, which was in line with observations by Coull (1990) and del Norte-Campos and Temming (1994).

Daily and annual consumption levels were estimated for the most abundant predator species (*n* = 30 ind. of each predator species, pooled over time and sites) in biomass (g AFDW) and energy units (J) using conversion factors (Table 1), based on the mean number per gut of each prey item (species or otherwise the lowest taxonomic level). The annual energy flow from benthic invertebrates to epibenthic predators, for the entire Culbin Sands lagoon, also took into consideration the median

epibenthic densities at each site, estimated visually from the top of the mussel beds (on areas 3 x 3 m; $n = 5$ per month), and these were extrapolated for similar habitats.

Finally, the consumption efficiency (%) was estimated as the annual consumption by epibenthic predators / standing stock of benthic invertebrate prey x 100. The consumption efficiency of other less-abundant predator species, which ingested mostly zooplanktonic species, were not estimated due to a lack of information on the standing stock of zooplanktonic communities at Culbin Sands.

In order to estimate the benthic invertebrate standing stock ($\text{g AFDW m}^{-2} \text{ yr}^{-1}$ or $\text{kJ m}^{-2} \text{ yr}^{-1}$) at Culbin Sands lagoon, benthic communities were studied from Feb. 1994 to Aug. 1996 on the intertidal flats, at the same 3 sites sampled for epibenthic fauna. Sediment samples were taken to a depth of 15 cm, from within a randomly placed 1 m x 1 m quadrat (Raffaelli and Hawkins 1996). A pilot survey, conducted at the beginning of the study, determined the minimum amount of samples which represented the benthic invertebrate macrofauna ($> 500 \mu\text{m}$) species density and diversity with 95% confidence. During this pilot survey, 10 corers (of 11 cm of diameter equivalent to an area of 100 cm^2) were collected at each site and showed that for most species, 6 corers were the minimum number of samples which needed to

be collected. Exceptions were species with patchy distributions. The mussel beds of *Mytilus edulis* were not studied, although they occupy about $18 \times 10^3 \text{ m}^2$ at Culbin Sands (Mendonça et al. 2008). Following the conclusions of the pilot survey, 6 corers were then collected per site every 2-4 wks from May 1994 to Aug. 1996. Samples were sieved through a $500 \mu\text{m}$ mesh and preserved in alcohol (70%) until identified. Corer sampling was inefficient for larger species such as lugworms *Arenicola marina*. So, densities of those species were estimated only in winter (Feb. 1995 and Feb. 1996) and summer (July 1995 and Aug. 1996) by counting the number of casts in 10 quadrats of $0.5 \text{ m} \times 0.5 \text{ m}$, randomly placed at each of the sites. All results were converted into ind./m^2 .

For both the consumption by epibenthic species and standing stock estimates, the mean individual DW was obtained from 30 individuals randomly selected from each size class considered. Individuals in samples were separated into size classes whenever possible. The maximum length of individuals were measured to the nearest micrometer, considering at least two classes: < 1000 and $\geq 1000 \mu\text{m}$; except for bivalves in which the maximum width was measured, and 5 size classes were considered: 500-1000, 1000-1500, 1500-2000, 2000-3000, and $> 3000 \mu\text{m}$. For species with a shell (bivalves and

Table 1. Conversion factors used to convert the biomass of the stomach contents of epibenthic predators into energy units. AFDW, ash-free dry weight; DW, dry weight; N/A, not applicable

| Taxa | Body size ^a (μm) | Conversion factor from DW to AFDW (Rumhor et al. 1987) | Energy content (J/mg) |
|---|--|--|--|
| Meiofauna | < 500 | 0.70 | 23.40 J in 1 mg DW (Ankar and Elmgreen 1976) |
| Nemertean | < 1000 | 0.70 | 23.40 J in 1 mg DW (Ankar and Elmgreen 1976) |
| Polychaetes | < 1000 | 0.70 | 22.36 J in 1 mg DW (Brey et al. 1988) |
| | ≥ 1000 | 0.30 | 23.33 J in 1 mg AFDW (Brey et al. 1988) |
| Oligochaetes | < 1000 | 0.70 | 22.36 J in 1 mg DW (Brey et al. 1988) |
| | < 1000 | 0.70 | 22.40 J in 1 mg AFDW (Brey et al. 1988) |
| Crustaceans | ≥ 1000 | 0.30 | 22.40 J in 1 mg AFDW (Brey et al. 1988) |
| Calanoid Copepods | N/A | 0.70 | 24.30 J in 1 mg DW (Comita and Schindler 1963) |
| <i>Crangon crangon</i> | N/A | 0.30 | 17.60 J in 1 mg DW (Evans 1983) |
| <i>Crangon crangon</i> eggs | N/A | 0.70 | 25.10 J in 1 mg DW (Edwards 1978) |
| Insects (Chironomids) | < 1000 | 0.70 | 23.81 J in 1 mg AFDW (Brey et al. 1988) |
| | ≥ 1000 | 0.30 | 23.81 J in 1 mg AFDW (Brey et al. 1988) |
| Bivalves | < 1000 | 0.15 | 22.79 J in 1 mg AFDW (Brey et al. 1988) |
| | ≥ 1000 | 0.10 | 22.79 J in 1 mg AFDW (Brey et al. 1988) |
| Fish (<i>Pomatoschistus</i> spp. eggs) | N/A | 0.70 | 25.10 J in 1 mg DW (Healy 1972) |

^aTotal width for crabs and bivalves; total length for worms and insect larvae; from eyes to telson for shrimps; from snout to tail end for fish.

gastropods) the shell-free dry weight (SFDW) was estimated. Gastropods (mostly *Hydrobia ulvae*) were not easily dissected from the shell because of their small size, so the flesh dry weigh (FDW) was estimated as 27% of the total DW, after Raffaelli and Boyle's (1986) study in Nigg Bay, also in the Moray Firth, although the flesh weight presented some degree of variation throughout the year. All materials were dried to a constant weight (at 70°C for 24 h in a laboratory oven). The DW was then converted into AFDW and then also into energy units using the conversion factors in table 1.

RESULTS

Spatial and temporal variability of epibenthic predators

Epibenthic species recorded at Culbin Sands lagoon included crustaceans (brown shrimp *Crangon crangon* and shore crab *Carcinus maenas*), starfish (*Asteria rubens*), and teleost fish (sandeel *Ammodytes* spp., sticklebacks *Gasterosteus aculeatus* and *Spinachia spinachia*, sea scorpion *Myoxocephalus scorpius*, pipefish *Nerophis lumbriciformes*, gobies *Pomatoschistus*

microps and *Pomatoschistus minutus*, and flatfish plaice *Pleuronectes platessa* and flounder *Platichthys flesus*). Brown shrimp *Crangon crangon* were the most abundant epibenthic species with densities of 10-100 ind./m². The most common fish species were *Pomatoschistus microps* and *Pleuronectes platessa*, both at densities of 1-10 ind./m². Other species occurred at densities of 0-1 ind./m².

All epibenthic specimens were relatively small (Figs. 2, 3), and larger sizes of the most common species only occurred during warmer months (Fig. 4). When compared with results for shrimp *Crangon crangon* and flatfish *Pleuronectes platessa*, a less-clear allometric relationship was observed in the goby sample. This is probably an indication that the sample included both *Pomatoschistus microps* and *Pomatoschistus minutus*, specimens of which in fact had a similar body size and caused some confusion, especially during summer when some individuals presented nuptial coloration.

Site 1, near major mussel bed areas, had a higher index of diversity of epibenthic species and included sandeel *Ammodytes tobianus*, 3-spined stickleback *Gasterosteus aculeatus*, 15-spined stickleback *Spinachia spinachia*, and

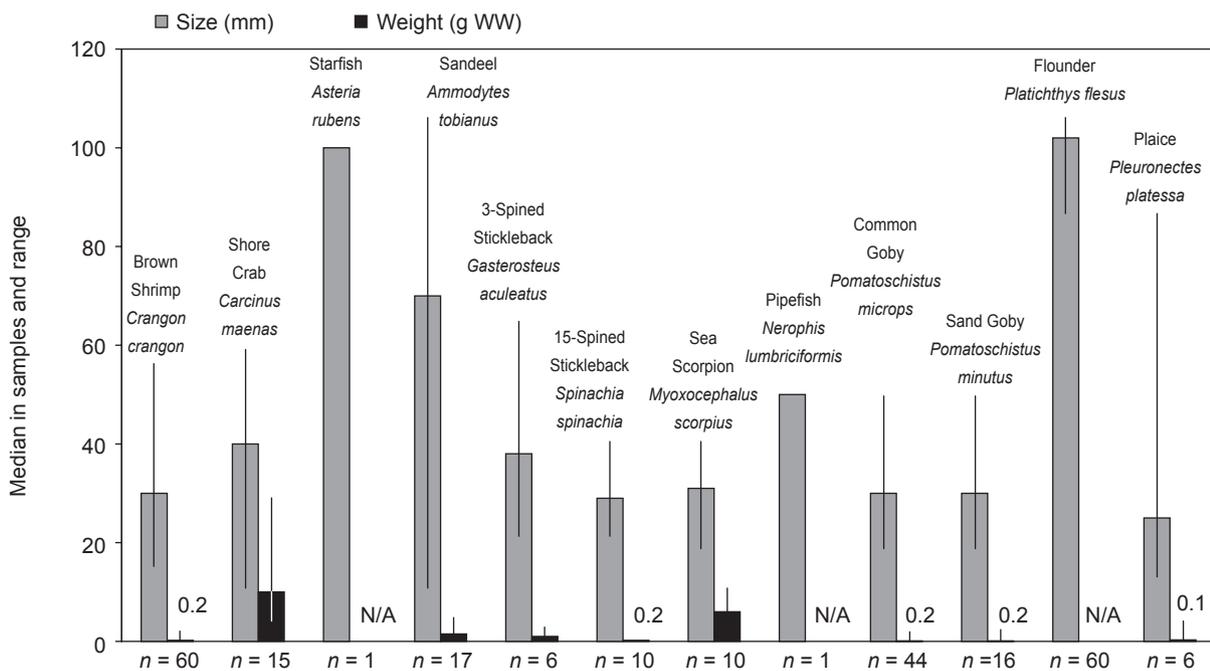


Fig. 2. Body size (from eye socket to telson for shrimp, total width for crabs, and from snout to tail end for fish) and wet weight (WW) of epibenthic species, sampled during 1994-1996 at Culbin Sands. For the most abundant species of brown shrimp, common gobies, and plaice, samples were pooled over sites and time.

sea scorpion *Myoxocephalus scorpius*, which were only recorded at this site. Shrimp and gobies were found at all sampled sites, while plaice was recorded in more-exposed areas (Fig. 5). The species composition at all sites also showed distinctions between summer and winter, with more species being recorded in summer (Fig. 6).

Diets of epibenthic predators and indices of relative importance of their prey

Diets of epibenthic predators included benthic infauna (especially polychaetes *Eteone longa*, *Pygospio elegans*, and *Fabricia sabella*; oligochaetes *Tubificoides benedini*; isopods *Eurydice pulchra*; and bivalves *Cerastoderma edule* and *Macoma balthica*), small epibenthic organisms (amphipods especially *Bathyporeia pilosa* and *Gammarus* sp., and juvenile crabs *Carcinus maenas* and shrimp *Crangon crangon*), and zooplankton (harpacticoids, ostracods mostly *Cypris* sp., calanoid copepods, mysids *Praunus flexuosus*, and eggs). Insect larvae (Chironomidae) were also frequent in stomach contents of epibenthic predators (Table 2).

Comparisons of the volumetric composition of prey in stomachs of epibenthic species showed that most common epibenthic species

(brown shrimp *Crangon crangon*, common goby *Pomatoschistus microps*, and plaice *Pleuronectes platessa*) were also predators with similar diets, feeding mostly on annelids, amphipods, and insect larvae (Figs. 7, 8).

The numerical composition and frequency of occurrence of prey for the most abundant epibenthic species are presented in table 3. However, prey items with higher indices of relative importance for the most abundant predators (brown shrimp, common gobies, and plaice) were chironomids for shrimp, amphipods *Bathyporeia pilosa* for shrimp and gobies, harpacticoids for plaice and gobies, and bivalve siphons mostly for plaice (Fig. 9).

Dietary items (volumetric composition) of *Crangon crangon* of larger than 20 mm did not significantly vary over time or among sites in 1994-1996 (P not significant when results were tested by 2-way ANOVA and Bonferroni test, $n = 15$ per site and month). Sand grains were found in shrimp stomachs but were not taken into account in the volume calculations. Larger shrimp (20-50 mm) also ingested significantly more *Bathyporeia pilosa* ($P = 0.02$, $F = 11.14$), mysids ($P = 0.038$, $F = 4.72$), and bivalve siphon tubes ($P = 0.018$, $F = 6.32$), and fewer chironomid ($P = 0.02$, $F = 5.52$) and bivalve larvae ($P = 0.01$, $F = 6.32$) than did

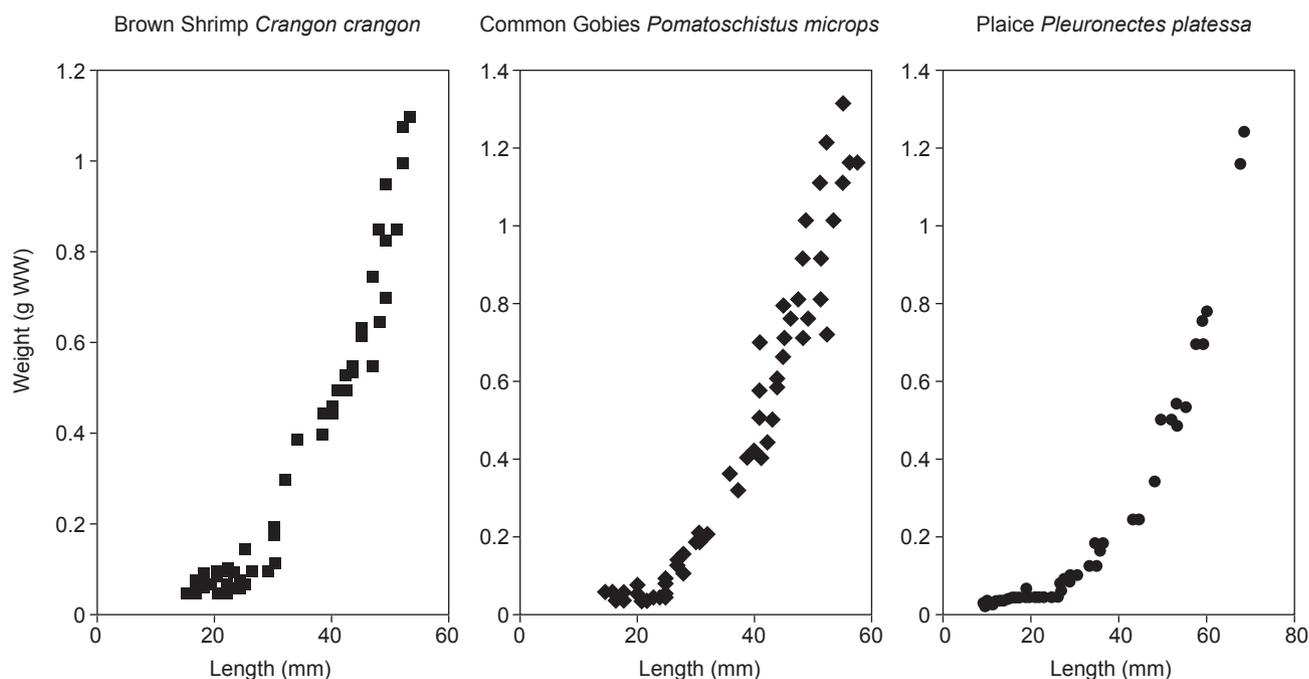


Fig. 3. Allometrics (length from eye socket to telson for shrimp and from snout to tail end for fish; WW, wet weight) of most common epibenthic species, sampled during 1994-1996 at Culbin Sands ($n = 60$ ind. per species, pooled over sites and time).

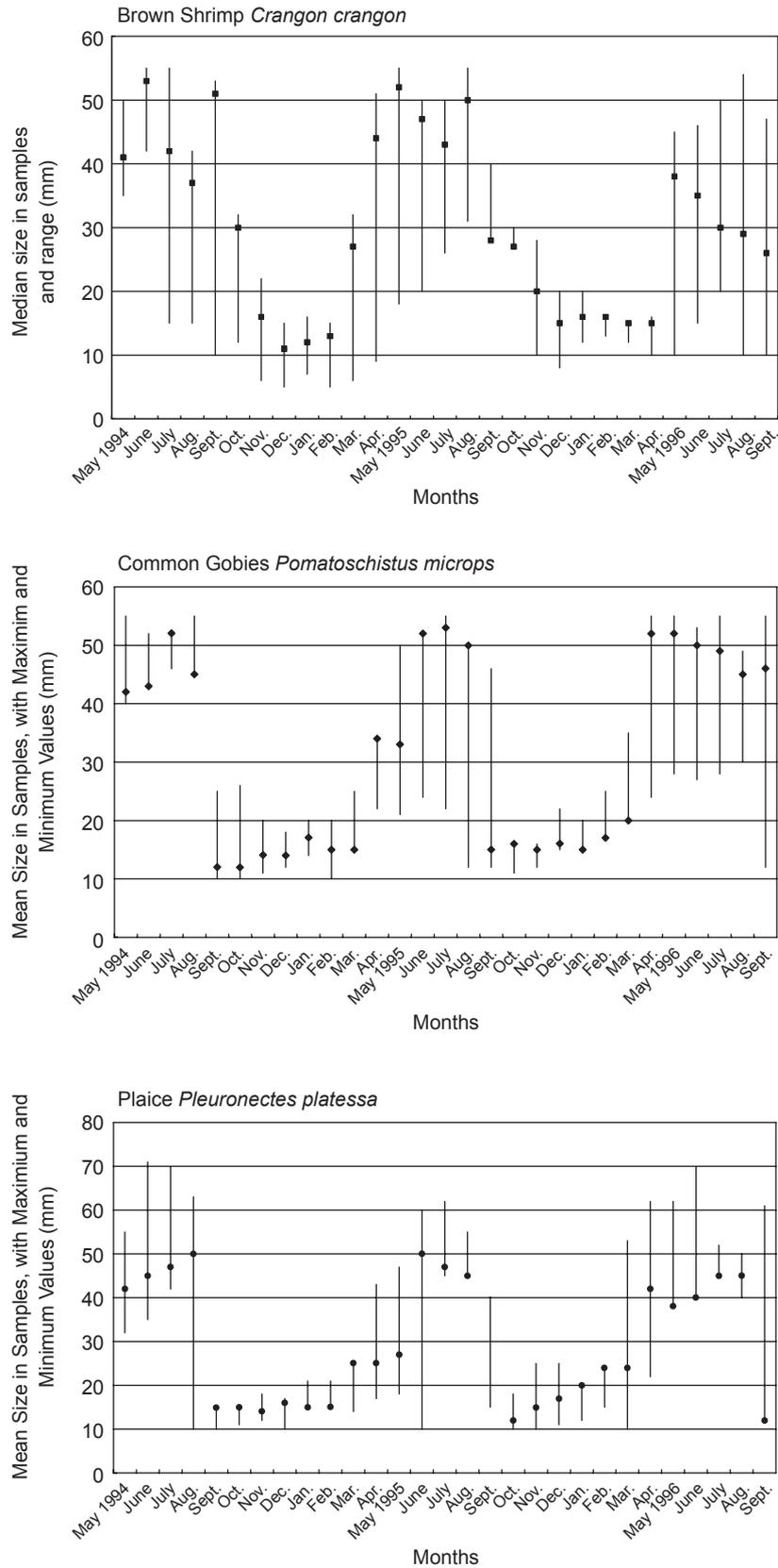


Fig. 4. Body size of most common epibenthic predators throughout the year, sampled during 1994-1996 at Culbin Sands ($n = 20$ ind. per species per month, pooled over sites).

smaller shrimp (1-way ANOVA and the Bonferroni test).

The majority of *Pomatoschistus microps* individuals sampled were about 35 mm in length, from snout to tail end; thus size categories were not considered. Diets (volumetric composition) of these individuals did not significantly vary over time or among the three sites, with respect to the major prey taxa identified (P not significant by 2-way ANOVA and the Bonferroni test; $n = 10$ per site and month). There were also no significant differences between the diets of the common goby *Pomatoschistus microps* and sand goby *Pomatoschistus minutus* (P not significant by 1-way ANOVA and Bonferroni test; $n = 15$ per species pooled over all sites and time). Sand grains were also found in stomachs of gobies, although not as often as in shrimp, and were not taken into account in the volume calculations. Gobies ingested mainly amphipods (*Bathyporeia* spp., *Corophium* spp., and *Gammarus* spp.), harpacticoids, polychaetes (especially *Pygospio elegans*), chironomid larvae and pupae, and bivalve siphons. Mysids, eggs and larvae of *Crangon crangon*, ostracods mostly *Cypris* sp., isopods *Eurydice pulchra*, calanoid copepods, oligochaetes, and cyprinid larvae were

also present in the guts in smaller amounts.

All *Pleuronectes platessa* individuals collected in this study were juveniles between 10 and 80 mm in length, from snout to tail end, and three size categories were considered: < 20, 20-50, and > 50 mm. Diets (volumetric composition) of individuals of 20-50 mm, did not significantly vary over site or time (P not significant; by 2-way ANOVA and the Bonferroni test; $n = 15$ per site and month), but only the mean percentage by volume of polychaetes ($P = 0.01$, $F = 4.99$) and bivalve siphons ($P = 0.04$, $F = 3.39$) significantly varied according to the fish size (1-way ANOVA and the Bonferroni test; $n = 15$ per size category pooled over sites and time, with each size category a different subgroup, also subjected to Tukey's pairwise comparisons).

Consumption efficiency of epibenthic predators

Daily ingestion rates of 1%, 3%, and 2.5% of body WW were respectively estimated for the brown shrimp *Crangon Crangon*, gobies *Pomatoschistus microps*, and plaice *Pleuronectes platessa*. This implies energy flows of 150, 68, and 65 $\text{kJ m}^{-2} \text{yr}^{-1}$, from benthic invertebrates to shrimp

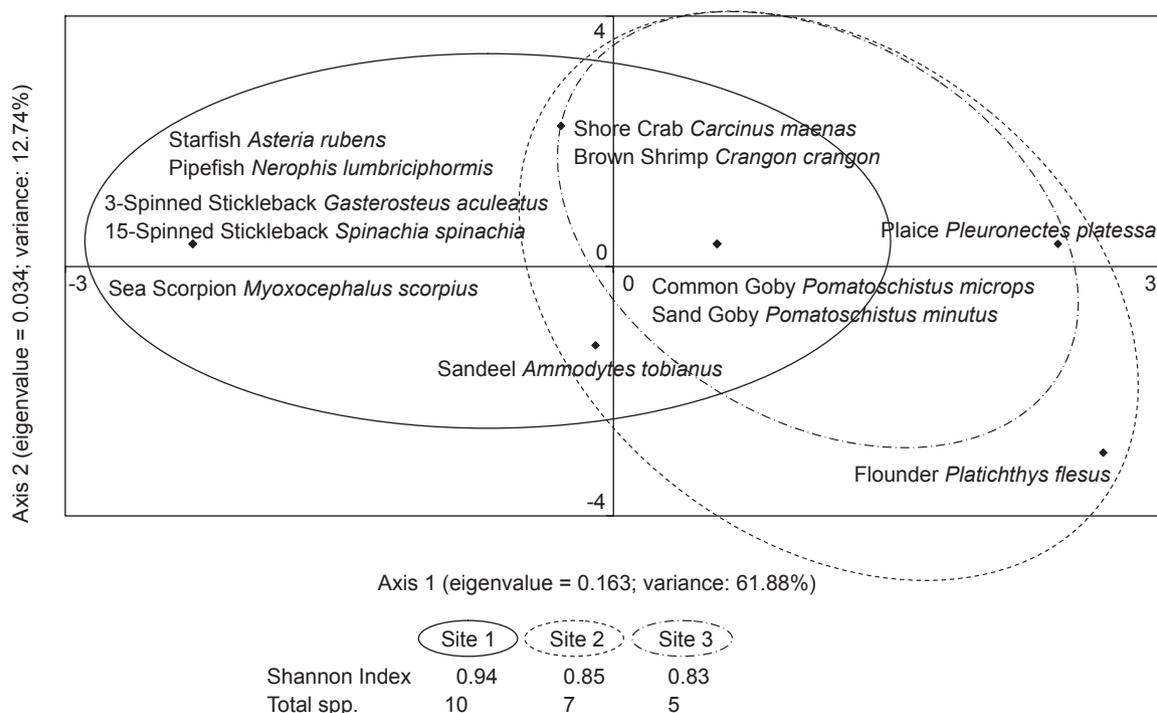


Fig. 5. Comparison of the 3 sampled sites during 1994-1996 for epibenthic species at Culbin Sands (by DECORANA test, only values along the 2 main eigenvalues were plotted here), with indications of diversity indices at each site.

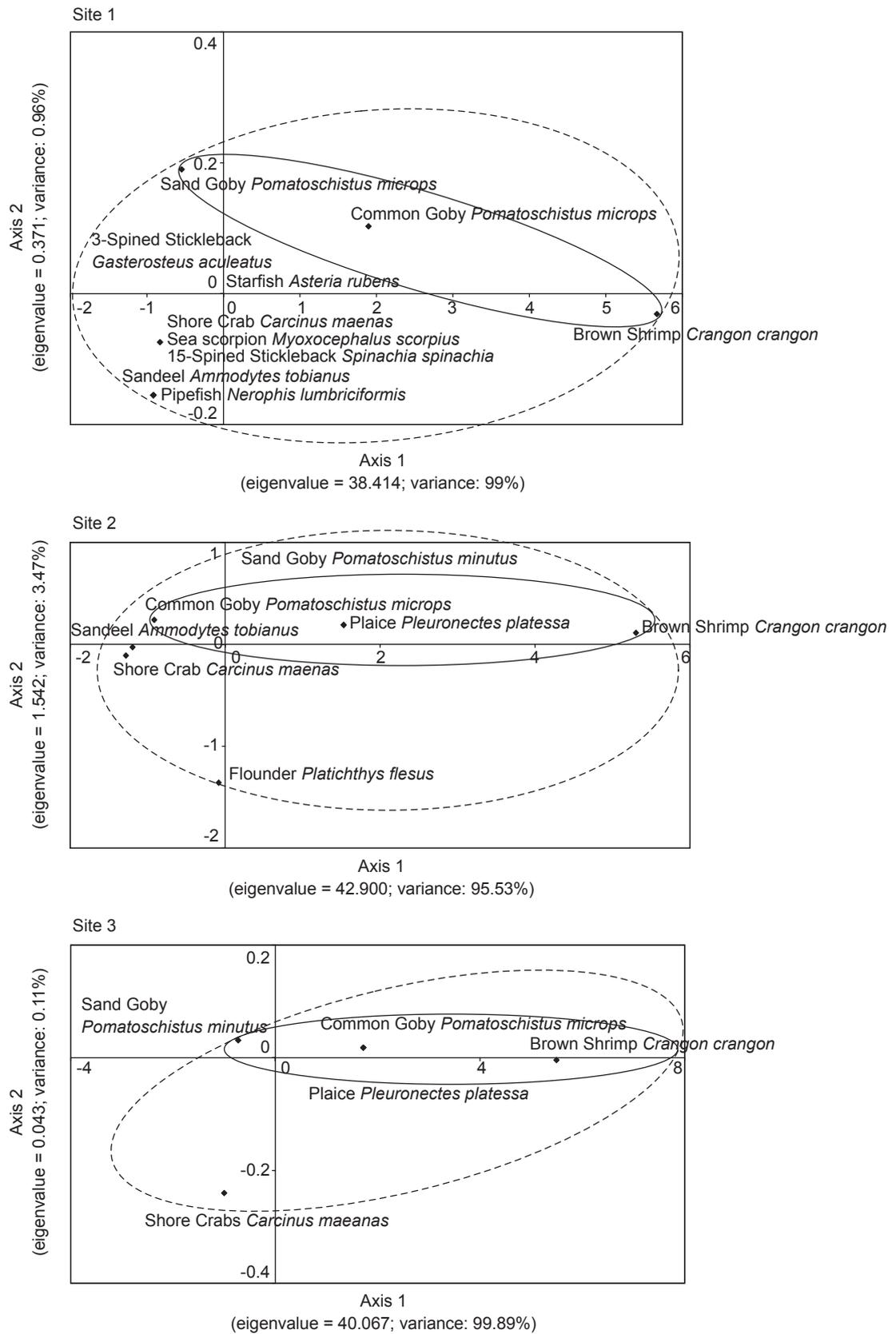


Fig. 6. Comparison of epibenthic species between summer (---) and winter (—) sampled during 1994-1996 at Culbin Sands (by principal component analysis, only values along the two main eigenvalues were plotted here).

Crangon crangon, goby *Pomatoschistus microps*, and plaice *Pleuronectes platessa*, respectively.

As the overall standing stock of benthic invertebrates during 1994-1996 was 500 kJ m⁻² yr⁻¹ or 26 g AFDW m⁻² yr⁻¹, the overall annual consumption efficiency by shrimp *Crangon crangon* was estimated as 30% of the available benthic invertebrate prey standing stock, while gobies *Pomatoschistus microps* and plaice *Pleuronectes platessa* each consumed 15% of the benthic invertebrate standing stock. These are equivalent to consumption efficiencies of 30%, 15%, and 15%, respectively for the shrimp, goby, and plaice.

Finally, although the standing stock of

small epibenthic species (such as the amphipod *Bathyporeia pilosa*), zooplanktonic organisms (harpacticoids, ostracods, and copepods), and chironomid larvae were not available for Culbin Sands lagoon, the consumption efficiencies of these prey could not be estimated, it is possible to argue that prey with higher indices of relative importance were species which provided the most important energy to epibenthic predators. For instance, most of the energy absorbed by shrimp came from amphipods and chironomids, most energy to gobies came from bivalves and zooplankton, and most energy to plaice came from polychaetes, bivalves, and zooplankton (Fig. 10).

Table 2. Diet composition of epibenthic species at Culbin Sands lagoon, during 1994-1996, based on stomach contents. N/A, not available

| Taxa (predator) | Body size ^a (mm and sample size) | Diets (Volumetric composition, %) |
|--|---|--|
| Crustaceans | | |
| Brown shrimp <i>Crangon crangon</i> | 15-50; n = 30 ^b | 50% amphipods, 20% chironomids, 5% annelids, 5% others (nematodes, mysids <i>Praunus flexuosus</i> , crabs, isopods, and bivalves) |
| Shore crab <i>Carcinus maenas</i> | 11-50; n = 15 | Polychaetes, harpacticoids, mysids, and bivalves ^c |
| Starfish | | |
| Common starfish <i>Asteria rubens</i> | 100; n = 1 | N/A |
| Teleost fish | | |
| Sandeel <i>Ammodytes tobianus</i> | 15-1150; n = 17 | 80% harpacticoids, 10% <i>Cypris</i> sp., 5% polychaetes, 5% others (amphipods, mysids, chironomids, and eggs (lamellaebranchs, acarine, and <i>Semibalanus</i> sp.)) |
| Three-spined stickleback <i>Gasterosteus aculeatus</i> | 22-56; n = 6 | 85% harpacticoids, 10% eggs, 5% chironomids |
| Fifteen-spined stickleback <i>Spinachia spinachia</i> | 25-34; n = 10 | 90% harpacticoids, 10% <i>Gammarus</i> sp. |
| Sea scorpion <i>Myoxocephalus scorpius</i> | 20-38; n = 10 | 35% <i>Crangon crangon</i> , 20% <i>Gammarus</i> sp., 15% <i>Bathyporeia pilosa</i> , 15% harpacticoids, 5% ostracods, 5% <i>Corophium</i> spp., 5% <i>Cypris</i> sp. |
| Pipefish <i>Nerophis lumbriciformis</i> | 50; n = 1 | N/A |
| Common goby <i>Pomatoschistus microps</i> | 11-55; n = 30 ^b | 30% annelids, 20% amphipods, 20% chironomids, 15% bivalves, 10% harpacticoids, 5% others (mysids <i>Praunus flexuosus</i> , isopods, cyprids, calanoids, <i>Crangon crangon</i> , ostracods) |
| Sand goby <i>Pomatoschistus minutus</i> | 11-50; n = 16 | 30% annelids, 20% amphipods, 20% chironomids, 15% bivalves, 10% harpacticoids, 5% others (mysids, isopods, <i>Cypris</i> sp., calanoid copepods, <i>Crangon crangon</i> , ostracods) |
| Flounder <i>Platichthys flesus</i> | 89-104; n = 6 | 80% <i>Crangon crangon</i> , 20% <i>Corophium</i> spp. |
| Plaice <i>Pleuronectes platessa</i> | 10-80; n = 30 ^b | 40% harpacticoids, 20% polychaetes, 15% bivalve siphons, 10% amphipods, 5% chironomids, 5% amphipods, 5% others (nematodes, ostracods, mysids) |

^aTotal width for crabs; from eyes to telson for shrimps; from snout to tail end for fish; ^bpooled over all sites and over time; ^call too fragmented to quantify.

DISCUSSION

Spatial and temporal variability of epibenthic predators

The higher predator abundances near mussel beds reflected not only higher prey densities (described in Mendonça et al. 2008),

but also because less-exposed conditions are suitable for reproduction of epibenthic species, and many empty bivalve shells provide ideal sites in which nests can be built. In fact, several male *Pomatoschistus microps* collected near mussel beds had nuptial coloration.

In line with the present study, Gunther (1996) also found higher biodiversity and abundance of epibenthic species near mussel beds, compared with open sandy areas, although he argued that shrimp *Crangon crangon* prefer sandy areas. In addition to that, *Crangon crangon*'s distribution may vary with water depth (Ueta 1996).

At Culbin Sands lagoon, some epibenthic species only occurred in samples during the warmer months. Even the overwintering epibenthic species were more abundant in summer, reflecting their life cycles, as in the North Sea adult epibenthic fish species, such as gobies migrate from the open sea to colonize shallower waters in spring, and flatfish return around the same time and in late autumn, when offshore waters become cooler and stormier (Modin and Pihl 1996). In addition to abiotic causes for fish migration, these species can also move in response to changes in food density over a time scale of days or weeks

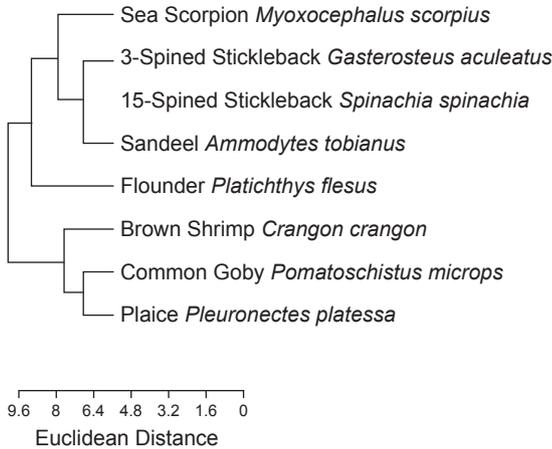


Fig. 7. Comparison of diets of epibenthic species at Culbin Sands (by cluster analysis).

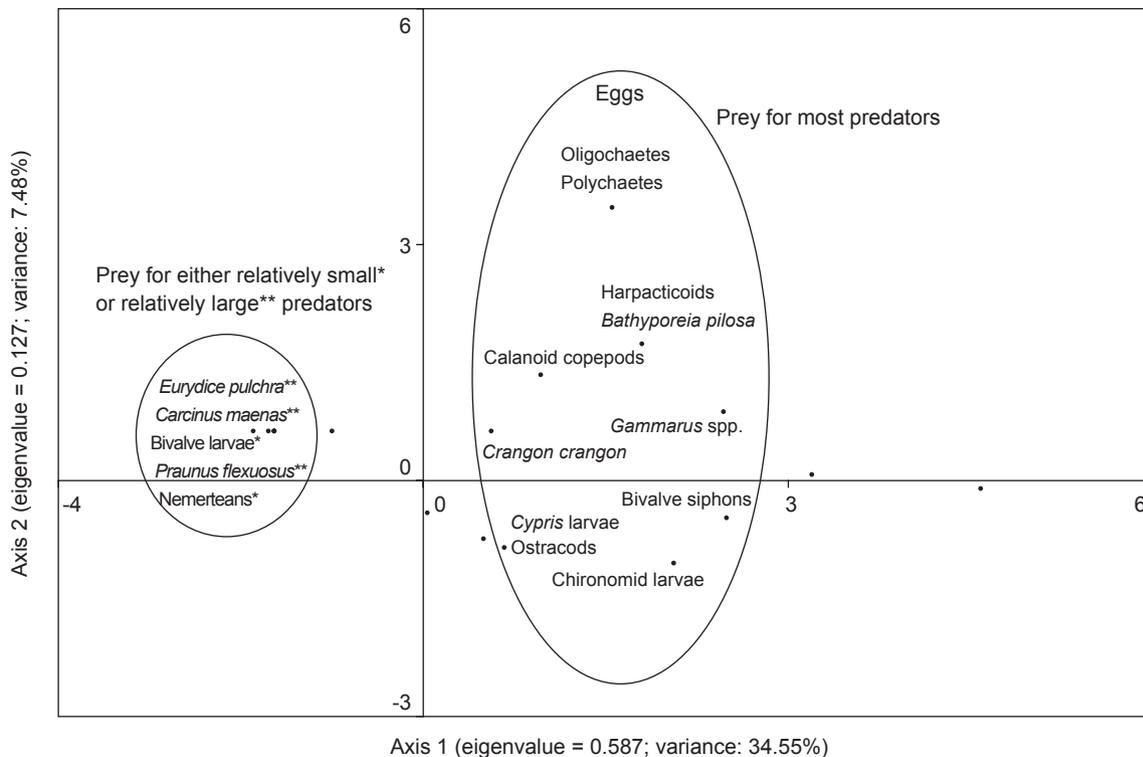


Fig. 8. Comparison of diets of epibenthic species at Culbin Sands showing the most conspicuous prey in predator stomach contents (by DECORANA test, only values along the 2 main eigenvalues were plotted here).

(Boddeke 1996). Shrimp *Crangon crangon* concentrations and distributions may also depend on predation pressure, because they are prey for many fish species such as larger flatfish (Taylor and Collie 2003).

The abundance of brown shrimp *Crangon crangon* was probably higher at Culbin Sands than in Scandinavian waters where several studies on shrimp production but also other epibenthic predators (such as gobies and plaice) have been carried out (ICES 2006). It is likely that the annual production of shrimp at Culbin Sands may also be slightly higher than that at other coastal ecosystems in NW Europe, due to warmer conditions often recorded in relatively shallow waters of the Moray Firth. This was also observed in other shallow waters of the UK such as the Forth estuary (Scotland) which is a nursery and overwintering area for North Sea fish species (ICES 2005). Plaice *Pleuronectes platessa* and flounder *Platichthys flesus* do not usually occur together, as flounders tolerate lower salinity values than plaice

(Green 1968). This probably explains why plaice individuals were more abundant at Culbin Sands, where there is little freshwater input to the lagoon. Plaice individuals were also more common at site 2 than at any other site, probably because this fish species requires open mudflats composed either of coarse sand or mud (Hayward and Ryland 1990), and sites 1 and 3 had many bivalve shells present, providing better habitats for gobies than for flatfish.

Other less-abundant epibenthic predators were found at very low densities at *Culbin Sands*. For instance, the shore crab *Carcinus maenas* which occurred at Culbin Sands at 0-1 ind./m² has been reported in the Forth estuary (Scotland) at higher densities in summer, although the mean overall density was only 0.0075 ind./m² (Mathieson and Berry 1997), while in the Gullmar Fjord (Sweden), its mean density was 3-5 ind./m² (Eriksson and Edlund 1977), but in the Ythan estuary (Scotland) densities of small crabs (< 20 mm) can reach 30 ind./m² (Raffaelli et al. 1989). Sandeel *Ammodytes tobianus* occurs in both

Table 3. Numerical composition (NC) and frequency of occurrence (FO) of prey in diets of most common epibenthic species (20-50 mm^a) at Culbin Sands lagoon. N/A, not available

| Taxa (prey) | | Brown shrimp | | Common goby | | Plaice | |
|-------------|-------------------------------|--------------------------|--------|-------------|--------|--------|--------|
| | | NC (%) | FO (%) | NC (%) | FO (%) | NC (%) | FO (%) |
| Nemerteans | unidentified | 12.13 | 43.33 | 0 | 0 | 0 | 0 |
| Polychaetes | unidentified | 7.51 | 30.00 | 0 | 0 | 0 | 0 |
| | <i>Fabricia sabella</i> | N/A | N/A | 2.65 | 10 | 14.67 | 43.33 |
| | <i>Pygospio elegans</i> | N/A | N/A | 21.23 | 30 | 3.40 | 26.66 |
| | <i>Scoloplos armiger</i> | N/A | N/A | 0 | 0 | 0.14 | 3.33 |
| | <i>Eteone longa</i> | N/A | N/A | 0 | 0 | 0.33 | 16.66 |
| | <i>Phyllodoce mucosa</i> | N/A | N/A | 0 | 0 | 0.77 | 3.33 |
| | <i>Cirratulus cirratus</i> | N/A | N/A | 0 | 0 | 1.59 | 10 |
| | <i>Capitella capitata</i> | N/A | N/A | 0 | 0 | 0.17 | 6.66 |
| | Oligochaetes | <i>Tubificoides</i> spp. | 5.79 | 16.66 | 0 | 6.60 | 0 |
| Crustaceans | <i>Bathyporeia pilosa</i> | 24.03 | 56.66 | 19.96 | 50.0 | 0.88 | 23.30 |
| | <i>Praunus flexuosus</i> | 1.11 | 5.00 | 0.47 | 6.60 | 0 | 0 |
| | <i>Eurydice pulchra</i> | 3.76 | 10.00 | 0.08 | 3.30 | 0 | 0 |
| | <i>Crangon crangon</i> | 0 | 0 | 1.67 | 3.30 | 0.42 | 6.66 |
| | <i>Carcinus maenas</i> larvae | 1.58 | 6.60 | 0 | 0 | 0 | 0 |
| | Harpacticoids | 0 | 0 | 26.19 | 46.6 | 43.73 | 86.66 |
| | <i>Cypris</i> sp. larvae | 0 | 0 | 0.17 | 6.60 | 0.28 | 6.66 |
| | Calanoid copepods | 0 | 0 | 6.67 | 3.30 | 0 | 0 |
| | Ostracods | 0 | 0 | 0.67 | 3.30 | 5.02 | 30 |
| | Insects | Chironomid larvae | 34.87 | 73.33 | 3.87 | 13.0 | 1.88 |
| Bivalves | unidentified larvae | 0.37 | 10.00 | 0 | 0 | 0 | 0 |
| | Cropped siphons | 4.06 | 20.00 | 4.07 | 16.00 | 17.15 | 76.66 |

^aFrom eyes to telson for shrimp; from snout to tail end for fish.

inshore and offshore waters in the North Sea, but they are more common in summer after the spring spawn (Hayward and Ryland 1990). Sticklebacks *Gasterosteus aculeatus* and *Spinachia spinachia*, although present at Culbin, are respectively known to prefer more-brackish waters or other food items such as macrophytes (Hayward and Ryland 1990) than those available at Culbin Sands.

Diets of epibenthic predators and indices of relative importance of their prey

Analyses of stomach contents of epibenthic species at Culbin Sands lagoon indicated that these predators ingested food both during rising and ebb tides. Similar results were also obtained by Jaquet and Raffaelli (1989). In addition to that, Pihl (1985) and del Norte-Campos and Temming (1994) recorded that *Crangon crangon* usually eats at dawn and very little at noon, while gobies eat in daytime, and at dusk and sunrise, consuming up to 3% of their body wet weight daily, in line with our results for Culbin Sands. Also in the Bering Sea,

juvenile fish have been recorded feeding even during dark hours (Schabetsberger et al. 2003). In fact, these daily patterns of activity and feeding in epibenthic species may be more important in atidal or micro-tidal areas, where tidal rhythms are less important, because it has been reported that in macro-tidal areas, these epibenthic predators tend to follow tidal rhythms and feed around high tide (Coull 1990).

In general, diets of epibenthic predators at Culbin Sands did not exactly match the results found elsewhere in waters off NW Europe. For instance, results from Pihl (1985) in Sweden showed that benthic macrofauna (bivalves, polychaetes, and crustaceans) were the major diet components of epibenthic predators, but at Culbin Sands, zooplanktonic crustaceans (harpacticoids and ostracods) were also frequently eaten by even-larger epibenthic predators such as flatfish. In addition to that, it was recorded by Rademacher and Kils (1996) that 15-spined sticklebacks *Spinachia spinachia* feed mainly on mysids, but at Culbin, this species ingested only harpacticoids

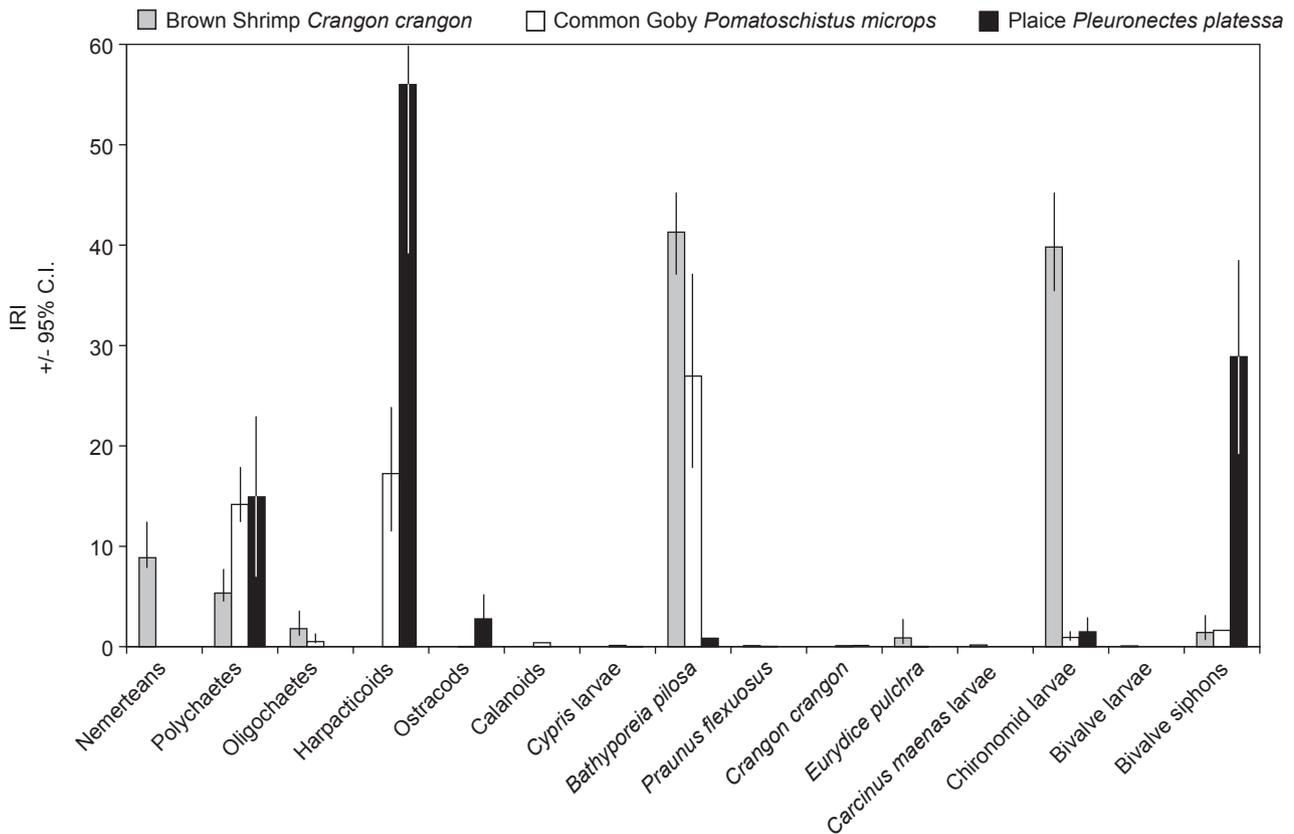


Fig. 9. Index of relative importance (IRI) of prey for the most abundant epibenthic species at Culbin Sands. Only prey with an IRI of > 1 are shown.

and *Gammarus* spp.

In fact, epibenthic species have been described as opportunistic predators, and may change their diet in response to hydrological parameters (Attrill and Thomas 1996) and prey availability (Heath 2007), and/or develop new prey-catching strategies. Moreover, intraguild predation may occur among members of the same guild that exploit the same resources (Krivan 2000, Matsumura et al. 2004, Tan and Romanuk 2004).

Despite that fact, it was clear from the present study that these predators had preferences for certain prey species. For instance, some prey which are not as abundant at Culbin Sands such as the polychaetes *Fabricia sabella* and *Eteone longa* were among the polychaetes with higher indices of relative importance in the diets of epibenthic species. This may also be related to the fact that these polychaete species had a

patchy distribution at Culbin Sands (Mendonça et al. 2008), so that predators concentrated on these patches. Additionally, the methods used to quantify most infaunal prey are not the best methods to study other benthic organisms such as the amphipod *Bathyporeia pilosa* which is also an epibenthic species, and chironomid larvae, the abundance of which would have been higher if the sampling method was directed at the meiofauna.

Consumption efficiency of epibenthic predators

Epibenthic predators were caught during the ebb tide, and some authors (Summers 1974) have stated that most feed mainly during the rising (flow) tide. In that case, some of the food may have already been digested at the time of sampling used in this study, and the harder, less-digestible prey items, would have been over-represented (facts

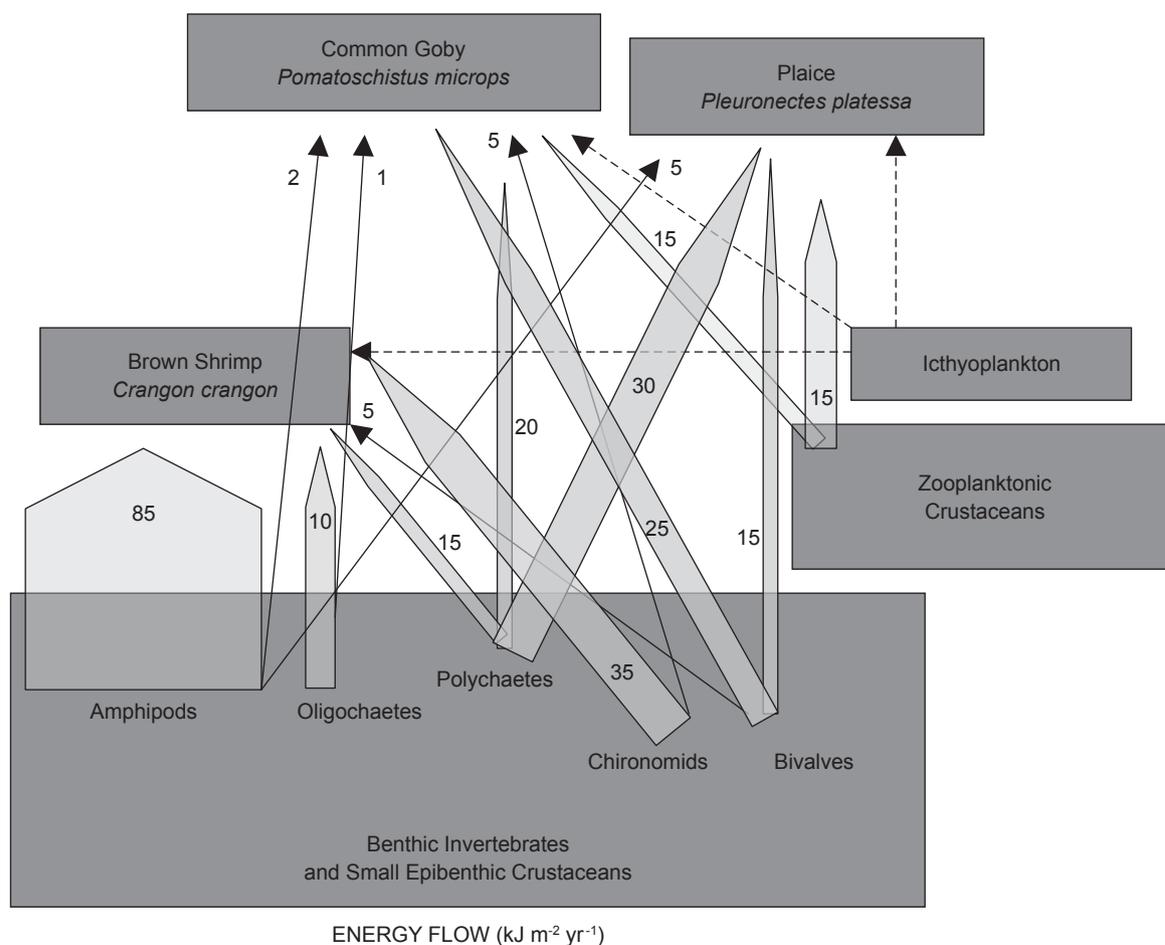


Fig. 10. Energy ($\text{kJ m}^{-2} \text{yr}^{-1}$) transferred annually from prey to the most abundant epibenthic predators at Culbin Sands, Moray Firth, Scotland. \rightarrow , indicates a residual flow from eggs and larvae.

taken into consideration in estimates of energy flow).

The annual consumption estimated for *Crangon crangon* at Culbin Sands lagoon was within the range of values found by Evans (1983) for a coastal area in Sweden, with similar sediment characteristics, although the consumption by epibenthic species at Culbin was lower than those recorded in muddier areas of the Ythan estuary, NE Scotland, outside the Moray Firth (Baird and Milne 1981).

On the other hand, values at Culbin Sands for *Pomatoschistus microps* were higher than those for *Pomatoschistus* sp. in the Gullmar Fjord, despite similar daily food intake levels. This difference could have been induced by the methods we used, as these estimates corresponded to sampled areas with higher predator concentration during low tide in the main gully, when predators are less spread out, so that goby densities, and thus annual consumption estimates, might have been overestimated.

Several arguments may be raised against the approach used in this study to measure the energy flow from prey to epibenthic predators, as estimates depended on stomach content analyses (and some prey may take longer than others to pass through the stomach), and were based on predator abundances and prey production. In fact, in the future, clearance rate and bioenergetics studies at Culbin Sands should also be complemented by studies using stable isotope techniques. Stable isotope ratios (typically of carbon and nitrogen) provide one representation of an organism's trophic niche, and are widely used to examine aspects of food web structures. Yet, stable isotopes only recently have been used to quantitatively characterize community-wide aspects of trophic structures (Dehn et al. 2007, Fontaine et al. 2007, Layman et al. 2007), but similar problems related to predator abundances and prey production may still arise.

Nevertheless, based on studies conducted at Culbin Sands, consumption of prey does not always reflect the impact of predators on their prey community density and structure, since predation does not necessarily mean mortality for the prey species, because often only a bite is taken off the prey (e.g., polychaete tails and bivalve siphon bites), and these chopped parts are easily regenerated (Sandberg et al. 1996). In addition to that, these prey species are generally known to have high mortality rates anyway, even without the intervention of predation.

In fact, complementary manipulative experiments at Culbin Sands showed that despite the estimated consumption efficiencies, the impacts of overwintering fish are not significantly detrimental to the prey community (Mendonça et al. 2007a), as demonstrated by caging experiments comparing areas accessed and not accessed by these predators (controls). In addition to that, further studies also showed that predation by shorebirds (Mendonça et al. 2007b) had stronger impacts on larger-sized benthic invertebrate communities than did epibenthic predators.

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