Untangling food webs helps us manage the estuary

Sound information on the feeding relationships within an estuary is crucial for understanding the ways in which that estuary functions. Ideally, such food webs describe not only which animal feeds on which food source(s), but how, from a dietary point of view, each of the main plant and animal groups are interrelated. These data, together with biochemical studies, then enable the ways in which energy is transferred within and among different trophic levels* to be determined.

The construction of food webs needs to take into account the fact that the food source of a species often changes as that species increases in body size. It should also recognise that, while some fish species are relatively specific in the types of food they consume, many of those found in estuaries are highly opportunistic in their feeding behaviour. Thus, the diets of fish can vary substantially within and more particularly among estuaries, according to the availability of the different potential food sources.

Reliable food webs provide the types of data that are required for refining environmental management plans for conserving the living resources of estuaries. For example, they enable environmental managers and scientists to predict the likely impact of the reduction or loss of certain predators or prey on the ecosystem, which may occur through the harvesting of those species or by changes in their habitats.

How do we know what fish eat?

The construction of a robust food web for an estuary requires good quantitative data on the dietary compositions of the various fauna found in that environment. These dietary data can be in the form of numbers, weights or volumes of the various items in the gut, which are then typically expressed as a percentage of the corresponding totals for those items. Most of the information on trophic levels, feeding groups and food items that is presented in this article has been derived from volumetric dietary data obtained over the last 30 years by research students and staff at the Murdoch University Centre for Fish and Fisheries Research. Some of the data is derived directly from the Swan–Canning estuary and some from other south-western Australian estuaries to help create a more complete food web.

The components of food webs in estuaries can be broadly allocated to one of the following four trophic levels.

1. **Primary producers.** Comprise mainly phytoplankton (microalgae found in the water column), benthic micro- and macroalgae, seagrass and other aquatic plants. For convenience, detritus, which consists mainly of decomposing plant material, is also included in this category.

* Technical terms highlighted in blue are defined in the glossary at the end of the document.
2. **Primary consumers.** Organisms that feed predominantly on primary producers. Examples include:

(a) **meiofauna,** i.e. very small **invertebrates,** such as nematodes (small worm-like animals) and certain **copepods,** that live on and in the (estuary floor) **substrate**

(b) small **benthic macroinvertebrates,** i.e. small invertebrates, such as **polychaete worms,** **gastropod** and **bivalve molluscs** and **amphipod crustaceans,** that live on or in the substrate

(c) **epibenthic** macroinvertebrates, i.e. larger invertebrates, such as prawns and crabs, that move more freely over the substrate surface than the previous group

(d) fish

(e) **zooplankton,** i.e. very small invertebrates, such as calanoid copepods and the larval stages of other invertebrates, that are found floating in the water column

(f) **surficial fauna,** i.e. insects that fall on the water surface, such as flying ants

3. **Secondary consumers.** Animals that feed mainly on the primary consumers. These comprise mainly small fish species, such as hardyheads and gobies, and larger fish species such as Yelloweye Mullet.

4. **Tertiary consumers.** Animals that feed to a large extent on secondary consumers. This group includes not only some of the larger fish species, such as Mulloway, Yellowtail Flathead and Tailor, but also birds, such as pelicans and cormorants, and humans.

Who eats what in the Swan estuary

Each of the fish species found in the Swan–Canning estuary and other estuaries in south-western Australia can be allocated to one of the six functional feeding groups listed in Table 1. Note that, in terms of the type of food ingested, some species straddle two groups. For example, a number of large fish species that feed on mobile benthic macroinvertebrates also ingest substantial amounts of fish.

We now describe the different sources of food for each of the above groups and provide selected examples of the organisms, and particularly the fish, which ingest those different sources of energy.

1. **Detritivores (feed on compost)**

Detritivores feed on decomposing plant material, which constitutes most of the detritus in estuaries. The detritus is derived mainly from either neighbouring land (typically fringing vegetation), tributary rivers or the estuary itself (aquatic macrophytes, micro- and macroalgae). The fine detrital particles found in and on the substrate constitute the main food for two fish species that are abundant in the Swan–Canning estuary, namely the Perth Herring *Nematalosa vlaminghi* and the Sea Mullet *Mugil cephalus.* Detritivores also ingest the considerable bacterial load that is associated with detritus and which can act as an extra energy source.

### Table 1 Functional feeding groups of fish and other aquatic animals.

<table>
<thead>
<tr>
<th>Feeding group</th>
<th>Food category</th>
<th>Consumer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Detritivores</td>
<td>Predominantly detritus</td>
<td>Adult Sea Mullet, Perth Herring, King and River prawns</td>
</tr>
<tr>
<td>Herbivores</td>
<td>Mainly macrophytes and filamentous algae</td>
<td>Eastern Striped Grunter, River Garfish, and the Black Swan</td>
</tr>
<tr>
<td>Benthophages</td>
<td>Predominantly meiofauna and the more sedentary benthic macroinvertebrates</td>
<td>Many fish species, including all whiting species, Estuary Cobbler, Blowfish, gobies, Common Silverbiddy, Western Gobbleguts, Elongate and Ogilby’s hardyhead, Yellowtail Grunter and Blue Swimmer Crab</td>
</tr>
<tr>
<td>Hyperbenthophages</td>
<td>Mobile, larger invertebrates living over the substrate</td>
<td>Flounders, flatheads, Australian Herring, Little Black and Little Pied cormorants</td>
</tr>
<tr>
<td>Planktivores</td>
<td>Mainly zooplankton, but occasionally also phytoplankton. Also flying insects that land on the water surface</td>
<td>Fish larvae, jellyfish, Australian Anchovy, Sandy Sprat and Mullet Hardyhead</td>
</tr>
<tr>
<td>Piscivores</td>
<td>Substantial amounts of fish</td>
<td>Flounders, flatheads, Australian Herring, Tailor, Mulloway, dolphins, cormorants and pelicans</td>
</tr>
<tr>
<td>Opportunists</td>
<td>Diverse range of food ingested (i.e. three or more of the above food categories) and dietary composition sometimes differs markedly between estuaries</td>
<td>Black Bream and Yelloweye Mullet</td>
</tr>
</tbody>
</table>
Coarse detritus is also sometimes ingested by those fish species that consume benthic or epibenthic prey, such as the Yelloweye Mullet *Aldrichetta forsteri* (Fig. 1), Yellowtail Grunter *Amniataba caudavittata* (Fig. 2) and the gobies *Favonigobius lateralis* and *Pseudogobius olorum*.

2. Herbivores (vegetarians of the estuary)

Herbivores feed on plants. The most common macroscopic plants found in south-western Australian estuaries are the seagrasses, e.g. the paddleweed *Halophila ovalis*, the eelgrass *Zostera marina* and the river reed *Ruppia megacarpa*, and macroalgae, e.g. the green algae *Cladophora montagneana* and *Chaetomorpha linum* and the red alga *Gracilaria verrucosa*.

A seasonal study of the dietary composition of the Yellowtail Grunter demonstrated that, in the upper Swan estuary, the juveniles of this species ingested large volumes of algae, and particularly *G. verrucosa*. However, the extent of this herbivory varied greatly with the time of year, with the volumetric contribution of plant material being as high as 50 per cent in summer but only about two per cent in spring.
Tarwhine *Rhabdosargus sarba* in the lower Swan estuary have been found to feed on increasingly greater amounts of seagrass as they increase in body size (Fig. 3). Recent studies have demonstrated that sparids, such as the Tarwhine, have the digestive enzymes required to break down this plant material and thus the ability to incorporate (assimilate) the released carbon.

The Black Swan *Cygnus atratus*, the faunal emblem of Western Australia, also feeds mainly on plant material and occasionally small benthic macroinvertebrates.

A detailed study of the Eastern Striped Grunter *Pelates sexlineatus* in the Peel–Harvey estuary during the 1980s (i.e. when that estuary was highly eutrophic and contained large amounts of macroalgae), showed that, under those conditions, this species fed almost exclusively on plant material. There appears to be no other fish species that feeds to such a large extent on plant matter in south-western Australian estuaries.

However, on the basis of studies elsewhere, the River Garfish *Hyporhamphus regularis*, which was previously relatively abundant in the Swan estuary, probably feeds largely on macroalgae.

3. Benthophages (feed off the estuary floor)

Benthophages feed on animals in (meiofauna) or on (benthic macroinvertebrates) the estuary floor.

Meiofauna (small and in the sediment)

The nematodes and very small crustaceans (mainly harpacticoid copepods) which live between the sediment grains, can act as an important food source for the newly settled juveniles of a variety of fish species, particularly whiting (e.g. King George Whiting, *Sillaginodes punctata*, Fig. 4), and for fish...
species that do not reach a large maximum size, such as the hardyheads and gobies that are abundant in south-western Australian estuaries (Figs 5 and 6).

**Benthic macroinvertebrates (most popular on the menu, found on the sediment)**

Benthic macroinvertebrates are the most important overall food source for fish in the estuaries of south-western Australia. Detailed studies have shown that the Swan River and Peel–Harvey estuaries and Wilson Inlet contain large numbers of a wide range of these invertebrates. This group includes polychaete worms, gastropods and bivalve molluscs and many different crustaceans.

**Polychaetes (marine worms)**

Polychaetes, which are colloquially termed marine worms, are segmented and possess a distinct head, thorax and abdomen. They have eyes and other sensory appendages on their head and parapodia (feet) on their bodies. The parapodia, which are used for swimming, bear chaetae (hairs) that provide traction and thus facilitate movement through the sediment and, in some species, help move water into burrows. These physical features vary in prominence between the different species.

The capitellid polychaetes (e.g. *Capitella capitate*) which are particularly abundant in the Swan River and other estuaries, are small, slender and resemble earthworms (Fig. 7). In contrast, another very abundant polychaete, the nereidid *Ceratonereis aequisetis*, has paddle-like parapodia with black chaetae and also has well-developed eyes and head appendages (Fig. 8). The abdomen of the much larger and more robust orbiniid polychaete *Leitoscoloplos normalis* possesses slender branchiae (gills) and prominent dorsal parapodia, which give this green organism a ‘ragged’ appearance (Fig. 9). The bloodworm *Marphysa sanguinea*, which has five head appendages and small comb-like lateral branchiae on its body, also lives in tubes in the sediment and is frequently used as bait by anglers (Fig. 10).

Polychaetes make a substantial contribution to the diets of some fish species that are abundant in the upper Swan estuary, and particularly to those of Yellowtail Grunter and Black Bream *Acanthopagrus butcheri*, contributing about 15 per cent to the dietary volumes of those two species. Of those polychaetes, *C. aequisetis* and *M. sanguinea* are the most important, reflecting their relatively high densities in that part of the estuary. Polychaetes, mainly *C. aequisetis* and *L. normalis*, also made a considerable volumetric contribution, almost 20 per cent, to the diets of Western Gobbleguts *Apogon rueppellii* in the lower Swan estuary. This reflects the fact that these invertebrates are often associated with seagrass and that this fish species is often abundant in those habitats.

The whiting species that are common in estuaries, such as the Yellowfin Whiting *Sillago schomburgkii*, Trumpeter Whiting *S. burrus* and King George Whiting *S. punctata*, have been shown to consume large amounts of polychaetes, and particularly the nereidid *C. aequisetis*, in the Swan–Canning estuary, Wilson Inlet and local nearshore marine waters.
The ability of whiting to ingest large amounts of polychaetes is facilitated by their small and protrusible mouth, which enables them to ’suck up’ this food source.

**Gastropods**

The main types of molluscs in estuaries are gastropods (sea snails) and bivalves. The most abundant gastropods in the Swan–Canning estuary include *Nassarius burchardi* and *Velacumantus australis*, which have heavy dark shells and move freely on the substrate surface (Figs 11 and 12). The relatively large size of these gastropods presumably accounts for their small contributions to the diets of fish in estuaries. However, gastropods such as *Philine angasi*, which have a reduced and/or thin shell, comprise about five per cent of the dietary volumes of Yelloweye Mullet and King George Whiting in Wilson Inlet.

**Bivalves**

*Arthritica semen* is a small bivalve which lives just beneath the substrate surface and can be eaten by small fish species, such as gobies, and the smaller individuals of larger species, such as Yelloweye Mullet (Fig. 13). It can also be eaten in large quantities by the Blue Swimmer Crab *Portunus pelagicus*.

The large bivalves that are common in estuaries of south-western Australia include the sunset shell *Sanguinolaria biradiata*, the triangle shell *Spisula trigonella* (Fig. 14), the small mussels *Musculista senhausia* (Fig. 15) and *Xenostrobus* spp., and the large and relatively thick-shelled ‘clams’ such as *Tellina deltoidalis* and *Venerupis crenata* (Fig. 16). The muscular foot of the sunset shell often protrudes some distance from the edge of their shells, and the long and muscular siphons of the ‘clams’, which are tubes used for feeding and/or respiration, can be extended into the water above the sediment surface. These structures are often nipped off by fish such as King George Whiting, Trumpeter Whiting and Western Gobbleguts. The Estuary Cobbler *Cnidoglanis macrocephalus*, which is abundant in Wilson Inlet, is one of the few fish species to ingest large amounts of the thick-shelled *T. deltoidalis* and *V. crenata*, but does so only when it has reached lengths in excess of 0.45 m.
the biology of Estuary Cobbler in the Swan–Canning estuary between 1982 and 1984, when this fish species was abundant in that system, showed that the sunset shell was far more important in their diets than either of the two ‘clam’ species, which may reflect its greater ‘palatability’.

In the Swan–Canning estuary, Black Bream feed to a very large extent on the benthic molluscs *Xenostrobus* spp., which are relatively abundant in that system. These molluscs, as well as the zebra mussel and the sunset shell, also make substantial contributions to the diets of the Blowfish *Torquigener pleurogramma*.

**Crustaceans**

Small peracarid crustaceans such as amphipods and tanaids, are also typically abundant on the substrate of south-western Australian estuaries. Some of these crustacean species, such as the corophioiid amphipods *Corophium minor* and *Grandidierella propodentata* (Figs 17 and 18) and the tanaid *Tanais dulongii* (Fig. 19), are strong swimmers and are also active just below the substrate surface, or can construct tubes within the sediment. Some amphipods are also associated with mats of the red algae *Gracilaria verrucosa*.

Amphipods can reach high densities in estuaries, and particularly in their shallow margins.

They form the major part of the diets of the juveniles of many larger fish species, including Estuary Cobbler, Black Bream, Smalltooth Flounder *Pseudorhombus jenynsii* and Tarwhine, and are important throughout the life of certain benthic smaller fish such as hardyheads and gobies.

**4. Hyperbenthophages (feed on larger, moving animals on the estuary floor)**

Hyperbenthophages feed on larger mobile animals (crustaceans) on the estuary floor. These include carid decapods or shrimp (e.g. *Palaemonetes australis*) and spider crabs (e.g. *Halicarcinus ovatus*, Fig. 20), which live on or just above the substrate and can reach high densities in south-western Australian estuaries. Two small fish species, the hardyhead *Atherinosoma elongata* and the goby *Afurcagobius suppositus*, and other larger...
fish species, such as the Southern Bluespotted and Yellowtail flatheads (*Platycephalus speculator* and *P. endrachtensis*, respectively), Smalltooth Flounder and Australian Herring (*Arripis georgianus*), and birds such as the Little Black and Little Pied cormorants (*Phalacrocorax melanoleucush* and *P. sulcirostris*, respectively), eat large amounts of carid decapods, while larger Black Bream consume spider crabs. It is likely that carid decapods and/or spider crabs are also important in the diets of other fish species for which there is little dietary information, such as Tailor *Pomatomus saltatrix* and Mulloway *Argyrosomus japonicus*.

The River Prawn *Metapenaeus dalli* is consumed in small amounts by Smalltooth Flounder and Yellowtail Flathead in the Swan–Canning estuary.

5. Planktivores (feed on zooplankton and floating insects)

Planktivores eat mainly zooplankton but also phytoplankton and floating insects.

The members of the zooplankton community, and particularly very small copepods, are typically abundant in the upper part of the water column in both shallow and deeper waters of south-western Australian estuaries. Zooplankton form a large and essential component of the diets of the larvae of those fish species that reproduce within the estuary or in nearby marine waters. Such species include the Yellowtail and Southern Bluespotted flatheads and the Black Bream, all of which reach a relatively large size, and the Australian Anchovy *Engraulis australis*, Sandy Sprat *Hyperlophus vittatus*, Spotted Pipefish *Stigmatophora argus*, hardyheads (*A. elongata, Leptatherina presbyteroides* and *Leptatherina wallacei*) and gobies (*P. olorum, F. lateralis* and *A. suppositus*) which are relatively small. The smaller species that are found in deeper waters, such as the Australian Anchovy, continue to feed on zooplankton throughout life, while those fish species that are abundant in the shallow waters also ingest other prey.

Flying insects, and particularly ants, which alight on the water surface during certain times of the year, provide an additional food source for the hardyhead *L. wallacei* and juveniles of Australian Herring.

6. Piscivores (feed on fish)

Piscivores eat fish. Southern Bluespotted and Yellowtail flatheads, Smalltooth flounder and
Australian Herring eat moderate to large amounts of fish in addition to eating carid decapods. Their fish prey are typically small, such as gobies or hardyheads, or the juveniles of larger fish species, such as Western Gobbleguts. Other fish species in south-western Australian estuaries, such as Mulloway and Tailor, feed to a large extent on fish. However, due to the lack of quantitative dietary information on these last two species, it is difficult to determine the importance of such fish prey over their whole life cycle. Little Black and Little Pied cormorants eat moderate amounts of fish, while Pied and Black cormorants (Phalacrocorax varius and P. carbo, respectively), feed almost entirely on fish, and can thus compete with fish-eating fish.

7. Opportunists (not fussy eaters)

Opportunists eat food from three or more of the food categories discussed above. The two main opportunists in the Swan–Canning estuary are Blowfish and Black Bream.

**Slow food for the humble Blowfish**

Detailed sampling of the fish fauna of the Swan–Canning estuary that was undertaken between 1977 and 1986 by Murdoch University provided, among other things, important information about the diets of the Blowfish. This fish species, which are often very abundant in the shallows of the middle and lower regions of the estuary, were shown to feed opportunistically on a wide variety of benthic macroinvertebrates, including polychaetes, small amphipods and tanaid crustaceans, spider crabs, small and large bivalves and gastropods. The ingestion of such prey, which are typically sessile or slow-moving, presumably reflects the ‘slow’ overall swimming speeds of the members of this fish family, while the consumption of bivalves is made possible by the fact that they have hard, crushing mouthparts. Despite popular opinion, River Prawn were never found in the guts of this species.

**See food and eat it – the highly opportunistic Black Bream**

Black bream, which is highly sought after by recreational fishers in the Swan–Canning estuary, is also abundant in other estuaries in south-western Australia. Its diets have been examined in eight different water bodies along this coast, namely the Moore River estuary, Swan–Canning estuary, Lake Clifton, Normalup/Walpole Inlet, Wellstead estuary and the Stokes, Broke and Culham inlets. A collation of these studies has demonstrated that Black Bream is a highly opportunistic feeder, with its variable diet depending on the types of potential food that are available in those water bodies.

Black Bream feeds on a wide range of animal prey, but sometimes also consumes large volumes of plant material. For example, the macroalga C. linum comprised almost 40 per cent of the dietary volume of this fish species in the Wellstead estuary and macrophytes collectively contributed about 50%. In contrast, Black Bream consumes only small amounts of macrophytes in the Swan–Canning estuary, presumably reflecting the difference in overall abundance of macrophytes in those two estuaries.

Differences in the growth rates of Black Bream among estuaries are considered to be related, in part, to differences in the main types of food available. For example, the growth rate of juvenile Black Bream has been shown to be particularly slow in the Moore River estuary, which may be partly due to the fact that they feed to a greater extent on macroalgae than those juveniles in other systems along this coast, which feed largely on a range of small animal prey. This view is consistent with the fact that, when juvenile fish from the Moore River estuary were cultured in aquaria, they grew at the same rate as those from the Swan–Canning estuary.
A generalised food web for the Swan estuary

The food web shown in Fig. 21 reflects the most important dietary relationships between the main members of the fish fauna of the Swan–Canning estuary and the other living components of this system. To help in interpreting the relationships, the food web shows the four main trophic levels, i.e. primary producers and primary, secondary and tertiary consumers.

Summary

The above descriptions of the main feeding designations of fish in south-western Australian estuaries demonstrate that some fish species remain within the same designations throughout most of their life, such as the detritivore Sea Mullet, the herbivore Yellowtail Grunter and the planktivore Australian Anchovy, while other species fall within two or more feeding designations during their lifetime. This ‘plasticity’ reflects, among other things, (1) changes in the dietary compositions of fish as they increase in body size and (2) the ‘opportunistic’ nature of fish feeding, in that some species, such as Black Bream and Yelloweye Mullet, respond strongly to changes in the potential food supply. Thus, when interpreting dietary relationships among fish, information on their overall biology and habitats should always be taken into account.
There is limited dietary information for certain fish species that are common and/or reach a large size in the Swan–Canning estuary, which includes Australian Anchovy, Eastern Striped Grunter, Common Silverbiddy, Tailor, Mulloway and Australian Giant Herring. Further studies of their dietary compositions are thus needed to facilitate the production of a more complete food web for this estuary.

Further reading


Gill, HS & Potter, IC 1993. ‘Spatial segregation amongst goby species within an Australian estuary, with a comparison of the diets and salinity tolerance of the two most abundant species.’ Marine Biology 117, 515–526.


Kanandjembo, AN 1998. Fish and macrobenthic faunas of the upper Swan Estuary: interrelationships and possible influence of a dinoflagellate bloom.

M Phil thesis, Murdoch University.


Platell, ME, Orr, PA & Potter, IC 2006. ‘Inter- and intraspecific partitioning of food resources by six large and abundant fish species in a seasonally open estuary.’ Journal of Fish Biology 69, 243–262.


Tanaid – small, shrimp like, bottom dwelling, usually marine and brackish water crustacean.

Trophic level – groups of organisms that occupy the same position in a food chain e.g. primary consumers such as River Garfish, Black Swans and marine worms.

Zooplankton – very small animals that float or swim in the water column.

Glossary

Algae – group of aquatic plants containing chlorophyll and other photosynthetic pigments.

Amphipod – small crustacean (5 to 25 mm), also know as side swimmers.

Benthic – living on or in the bottom of the estuary (substrate).

Bivalve – animals with a shell hinged together e.g. mussels.

Copepod – micro-crustacean, usually less than 2 mm in size.

Crustacean – predominantly aquatic arthropods (segmented body and chitinous exoskeleton), includes crabs, shrimp, barnacles.

Decapod – crustacean having five pairs of walking legs

Detritus – decaying plant and animal material.

Epibenthic – living on the bottom of the estuary (substrate).

Eutrophic – having high microalgal or macrophyte growth due to high nutrients.

Filamentous algae – algae that grow in strands, having a fine thread-like appearance.

Gastropod – animals with a single shell (e.g. seasnail) or with no shell (e.g. sea slugs).

Invertebrates – animals without back bones.

Macrophytes – multicellular plants that live in the water such as seagrasses.

Meiofauna – very small invertebrates.

Microphytobenthos – benthic micro-algae.

Molluse – animals with a soft body usually protected by a shell.

Peracarid crustaceans – crustaceans that are usually associated with soft sediments or macroalgal communities.

Phytoplankton – microscopic algae found in the water column, also known as microalgae.

Polychaete – marine worms.

Substrate – estuary floor.