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Herbivorous fishes

Geoff Jones

Only about 20 per cent of fishes on temperate rocky reefs are strictly herbivorous, consuming and assimilating only plant material, although many other species include algae in their diet. Herbivory appears to have evolved a number of times in a number of different families of fishes and is often restricted to only a few species within any particular family. For example, of the 10 species in the Family Odacidae in Australian waters, only one species, the Herring Cale (*Odax cyanomelas*) is a herbivore. In contrast, there are six species of drummers (Family Kyphosidae), all of which appear to consume only algae. Other groups, such as blackfishes (Family Girellidae) and sea carps (Family Aplodactylidae), primarily consume algal material, but may be better described as omnivores. While most damselfishes (Family Pomacentridae) have a planktivorous feeding mode, there are eight species of scalyfins (genus *Parma*) in Australia that are largely, but not exclusively, herbivorous (see Chapter 19). Other families, such as the leatherjackets (Family Monacanthidae), include many species with varied diets that also include algae.

While a diverse array of herbivorous fishes can be found in the tropics, including parrotfishes, surgeonfishes, rabbitfishes, angelfishes and blennies, only a few algal-eating representatives of these groups have colonised temperate waters. Surgeonfish of the genus *Prionurus* (sawtail surgeonfish) are common in subtropical areas of Queensland, northern New South Wales and offshore islands. Some other species, including the Convict Surgeonfish (*Acanthurus triostegus*) and Dusky Surgeonfish (*A. nigrofuscus*), are only found in temperate waters as juveniles. The Blue-barred Orange Parrotfish (*Scarus ghobban*) is one of the few tropical parrotfishes whose range extends into temperate waters, both on the New South Wales and Western Australian coasts. Thus, the evolution and importance of the herbivorous feeding mode in temperate waters is an enigma. Why

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A male Herring Cale, a common herbivorous fish found around southern Australia. It feeds only on large brown algae. New South Wales. *Rudie Kuiter*

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Rock Cale, a common herbivorous fish on exposed reefs of New South Wales. Merimbula. *Ken Hoppen.*

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Zebra Fish are easily identified by their barred colouration. *Rudie Kuiter*

is herbivory so much more important in the tropics? Why have many tropical species not managed to colonise temperate waters? And why does herbivory in temperate species have such an unusual distribution among families? We are only just beginning to grapple with these questions.

WHO AND WHERE ARE THEY?

Most of the herbivorous species in temperate waters come from strictly temperate families. The exceptions are the damselfishes and the drummers which are found throughout tropical latitudes. Herbivory in damselfishes is much more developed on coral reefs where this family of fishes has greatly diversified. One tropical species, the Western Gregory (*Stegastes obpreptus*), is common as far south as Rottnest Island, but is only associated with coral-rich habitats. Scalyfins are the only strictly temperate branch of this family. Low-finned Drummer (*Kyphosus vaigiensis*), the most abundant drummer on the Great Barrier Reef, can also be found as far south as Port Hacking in New South Wales. All other herbivorous species have a primarily temperate distribution.

While some herbivorous fish species are broadly distributed across southern Australia, including Herring Cale and Zebra Fish (*Girella zebra*), most have more restricted distributions. The Silver Drummer (*Kyphosus sydneyanus*) has an unusual distribution in that it is common in New South Wales, South Australia and southern Western Australia, but rare in Victoria and Tasmania. It is replaced by the Western Buffalo Bream (*Kyphosus cornelii*) along the West Australian coast between Cape Leeuwin and Coral Bay. As for most reef fishes, there tend to be eastern and western representatives of most herbivorous groups. For example, the Southern Sea Carp (*Aplodactylus arctidens*) can be found in Tasmania and Victoria, and as far as Kangaroo Island in South Australia. The Western Sea Carp (*Aplodactylus westralis.*) extends from Yorke Peninsula in South Australia around to Rottnest Island in Western Australia. A third sea carp species, the Rock Cale (*Crinodus lophodon*) replaces Southern Sea Carp in New South Wales.

Scalyfins are represented by the Big-scaled Parma (*Parma oligolepis*) and the Banded Parma (*P. polylepis*) in southern Queensland and New South Wales, White Ears (*P. microlepis*) and Girdled Scalyfins (*P. unifasciata*) in southern New South Wales, the Victorian Scalyfin (*P. victoriae*) is found along southern Australia and there are three species in Western Australia: Bicolor Scalyfin (*P. bicolor*), McCulloch's Scalyfin (*P. mccullochi*) and Western Scalyfin (*P. occidentalis*). There are two eastern representatives of the genus *Girella* found in the east: the Luderick (*G. tricuspidata*), which prefers sheltered reef conditions and the Eastern Rock Blackfish (*G. elevata*), which prefers wave-exposed reefs. They are replaced by the Western Rock Blackfish (*G. tephraeops*) in South and Western Australia. The discrete distributions of species across southern Australia appear to reflect discontinuities in the coastal current systems that act as a barrier to the transport of larval fishes from one side of Australia to the other.

▽ Rainbow Fish are abundant in kelp forests but unlike the other Australian *Odax* species, they are not a herbivore. Montague Island, New South Wales. *Rudie Kuiter*

HOW MANY ARE THERE?

Although there are few species of algal-feeding fishes, individual species can be very abundant in some locations. In Western Australia, for example, Western Buffalo Bream can account for a large proportion of the biomass of fishes in reef habitats. The local distribution and patterns of abundance of herbivorous species appears to be related to their preferred algal habitats. The number of Herring Cale in an area is correlated with the amount of Common Kelp (*Ecklonia radiata*). In contrast, the abundance of the Victorian Scalyfin increases where there is greater cover of smaller turfing algae and in New South Wales, the local distribution of White Ears is closely related to that of urchin-grazed Barrens Habitat.

Herbivorous fishes differ enormously in their behaviour and patterns of movement. At one extreme are some damselfishes which defend territories from members of the same species and other herbivorous species. In the Victorian Scalyfin, for example, both males and females defend territories that range in size from 3–30 m^2. Scalyfins are highly territorial towards other herbivorous species and where there are large aggregations of scalyfin territories, other herbivores can effectively be excluded. The reasons for these territories is explained in Chapter 19. In contrast, Western Buffalo Bream can be territorial but are also found in large schools. In shallow water, individuals of both sexes can defend polygon-shaped territories of approximately 12 m^2. These territories contain turfing red algae but are bordered by large brown macro-algae, creating a matrix of polygons. In deeper water they appear to move along the edge of the reef in large schools.

WHAT DO THEY EAT?

Many fishes may be primarily herbivorous as adults, but life does not always start that way. It is generally thought that this is so because of the greater need young fish have for protein (as with humans). Some species, such as the Western Buffalo Bream only develop into herbivores once they reach 30–40 cm. At this stage, they develop an elongated gut with associated bacteria, which appear to be necessary to digest the cellulose contained in algae. Some species are not strict vegetarians even as adults. In the Eastern Rock Blackfish, for example, only 70 per cent of the diet consists of algae with the remainder made up of crustaceans. Whether this mix is determined by the degree to which the plant is fouled is unknown. In New South Wales, both the Southern Sea Carp and Ludetick feed mainly on understorey and epiphytic red algae, but can consume animal matter.

Many adult herbivorous fishes appear to have highly specialised algal diets. Girellids consume primarily red and green algae, although in most fish there is a small animal component (~15 per cent). Kyphosids, on the other hand, are strict herbivores, consuming a range of red, green and brown algae and are sometimes quite specialised in their diets. For example, Western Buffalo Bream exclusively eat red algae as adults and Herring Cale eat only brown algae, mainly the Common Kelp. It appears to preferentially consume tissue from the primary lamina, whereas the related New Zealand species, the Butterfish (*Odax pullis*) appears to show some selection for reproductive structures located on the secondary laminae. Strangely, the other *Odax* species found on Australian reefs, the Rainbow Fish (*O. acroptilus*) is a carnivore which specialises in eating the small snails that live on kelp plants.

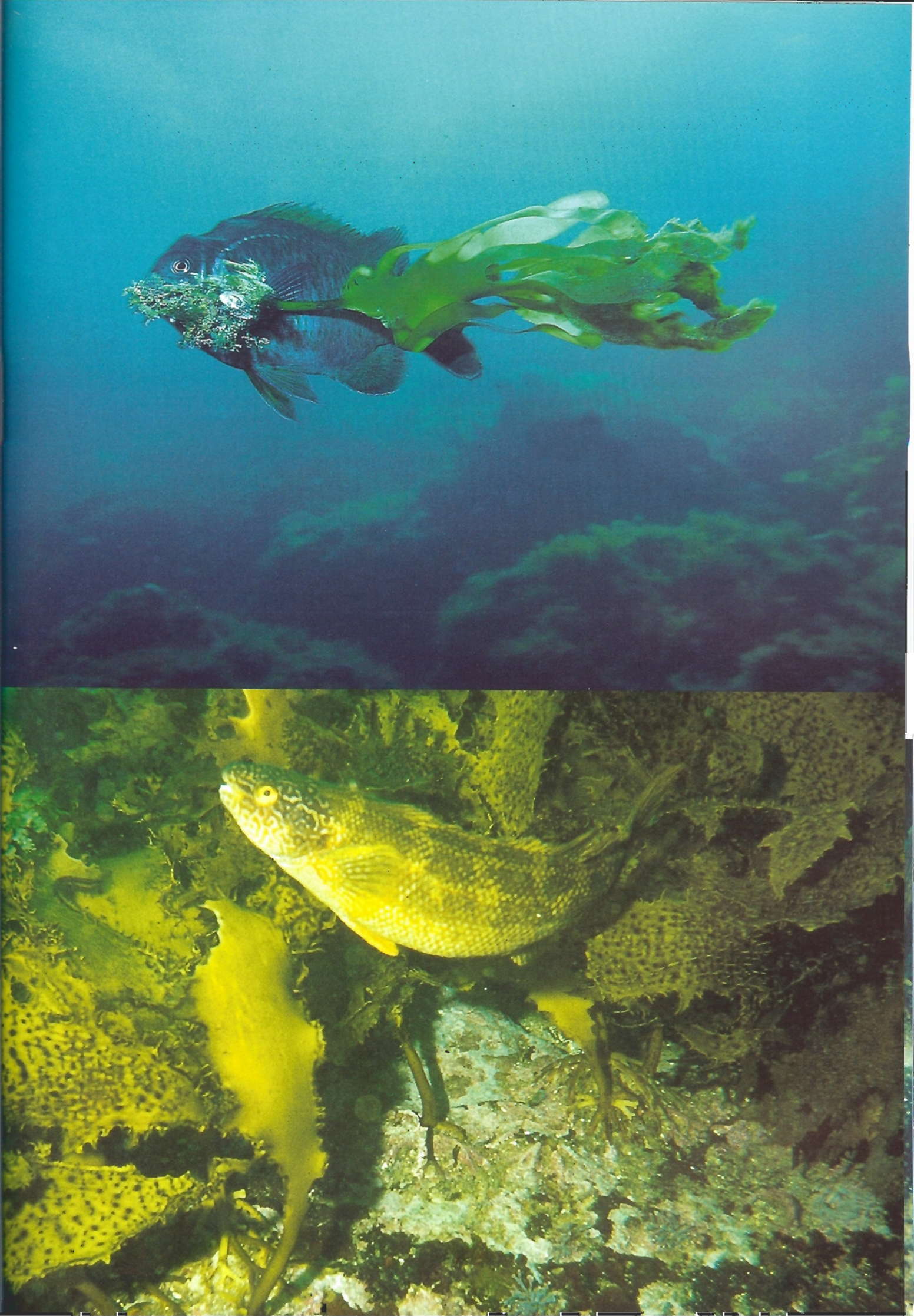
Other species of herbivores are capable of consuming a range of algal types, although they have strong preferences for certain species. For example, the Victorian Scalyfin consumes over 80 species of red and green algae, but has a strong preference for certain fleshy red algal species such as those in the genera *Champia* and *Rhodoglossum*. Individuals defending larger territories appear to have a greater consumption of these preferred species than those on small territories. However, when circumstances arise they can expand their territories to increase the supply of preferred food types. Similarly, sea carps can have highly flexible diets, but their reproductive success is reduced when they are restricted to less preferred species.

HOW DO THEY INGEST AND DIGEST ALGAE?

Differences in diet among herbivorous fishes may in part be explained by differences in their teeth and jaw structure. Girellids and kyphosids, for example, have many rows of closely set teeth that they use for scraping algae from the rock surface or browsing on larger algae. These teeth can be rapidly replaced when they wear out. Sea carps have a wide mouth with numerous small pointed teeth with which they graze the short turfing algae from hard rock surfaces. Herring Cale, on the other hand, have teeth that are coalesced into a 'beak' with a sharp even cutting edge. They use this to excise pieces from the fronds of kelp

▷ Victorian Scalyfin removing drift Common Kelp from its territory. Pope's Eye, Victoria. *Geoff Jones*

▷ Female Herring Cale in the process of clearing a patch of Common Kelp. Note the distinctive bite marks on the plant below her. Sydney, New South Wales. *Neil Andrew*



plants. These pieces are then processed by the action of the phatyngeal apparatus. This structure, in the throat, has fine tooth ridges which chop ingested material into smaller fragments.

Herbivorous fishes typically have an elongated intestine that allows them to assimilate plant material. Howevet, in each group a unique method of breaking down the plant cell walls of the algae has evolved. The Luderick has a highly acid stomach and a characteristic set of micro-otganisms for digesting plant material. Kyphosids on the other hand, use microbial fermentation in the hindgut to assimilate cellulose. Herring Cale are interesting because they lack the obvious morphological specialisations for herbivory found in the other gtoups, such as a gizzard or elongated gut. However, they have dense concentrations of prokaryote and eukaryote microbes in their lower intestines, which appear to function in digestion.

WHAT IMPACT DO THEY HAVE ON ALGAL COMMUNITIES?

Although not diverse, the sheer abundance of herbivorous fishes in some places suggests they may have a significant impact on the amount of algae, and perhaps also the species of algae on reefs. On limestone platforms in Western Australia, for example, the Western Buffalo Bream appears to create a mosaic of patches of red turf-algae, which are separated hy stands of large brown algae. It is likely that they are weeding out the larger unpalatable species from within their territory to enhance the growth of the red algae upon which they feed. Herbivorous damselfishes may also be improving the supply of their food species in this way. The Victorian Scalyfin is capable of removing large brown algae from their territories, although they seldom consume this material. Also, by actively defending their territories from other herbivores they appear to be able to maintain a good supply of preferted plant species. Experiments have shown that preferred algae are rapidly exploited by roving herbivorous fishes, once the territorial fish are removed.

Perhaps the mosr dramatic example of the effect of an herbivorous fish on algae occurs on the New South Wales coast, where at certain times of the year, Herting Cale completely destroy large patches of kelp. We know when, where and how they do, but why they do so still remains a mystery. Each year between August and October, they appear to return to the sites and clear the same patches of Common Kelp by preferentially feeding on the growing region at the base of the primary frond. This means that the plant is destroyed rather than heing completely consumed. Patches cleared by Herring Cale are easily identified because for a short period they persist like a forest of tree trunks with no branches or leaves. However, the stipes eventually die and rot away, creating a large bare patch within the kelp forest. Not long afterwards, new kelp plants re-establish and grow to form a new kelp canopy, whicb is cleared again at the same time the following year.

Why do Herring Cale keep coming back year after year to clear the same patches? One explanation may be that they have a strong preference for one-yeat-old kelp plants. Once a patch is established, each year they will find a stand of plants aged one year ar exactly the same place. This hypothesis was tested by an experiment in which reseatchers cleared large patches of kelp in other places, thereby establishing new stands of algae containing plants aged less than one year. However, this had no effect on Herring Cale. They continued to return to their traditional feeding sites. It appears that the seasonal impact of Hetring Cale is due to a change in the behaviour of females during the spawning season. During the spawning season males defend territories and spawn with females within the territories. Females aggregate at traditional sites near the edges of the territories prior to spawning. Tbey seem to garher in greater numbets near some territories. We do not know whether this is directly because of some attribute of the male or because the location of the territoty is better. The clearings appear to be simply a by-product of this dense aggregation of females. Clearance of kelp may not occur at other times of the year because feeding is less concentrated during non-spawning periods.

WHY ARE THERE SO FEW TYPES OF HERBIVOROUS FISH?

Although there are isolated examples of abundant herbivorous species in temperate waters and of species having a major local impact on algal communities, these examples appear to be the exception rather than the rule. The role of herbivorous fishes is much less important than on tropical reefs where grazing fishes abound and have major impacts on algae. This returns us to the question of why so few species have invaded or evolved in temperate waters. One explanation seems apparent. Consuming plant material is known to be less nutritious than consuming a similar volume of animal matter and it is generally assumed that it is harder to

'make a living' feeding in this manner. Tropical species tend to feed on microscopic algae growing in a highly productive environment, which may account for the success of this feeding mode on coral reefs. Grazers with a generalised feeding mode may be able to successfully exploit this food source. The productivity of these kinds of algae appears to decline in tempetate waters, which may explain why parrotfishes and other tropical species have nor invaded cooler waters. In parr, this may be because the rock surfaces where micro-algae grow are shaded by larger kelp species. Thus, to explain why tropical fishes have not invaded temperate waters we might have to first ask the question of why kelp plants have not become widely established in the tropics.

*Unlike their tropical counterparts, temper*ate herbivorous fish generally consume tissue from larger plants and could be considered browsers (taking distinct bites from individual plants) rather than grazers (consuming bits of many individual plants in the same bite). Temperate waters clearly support large standing stocks of macto-algae that would appear to be an abundant source of food. But is it? It appears that many large algal plants contain toxins or other metabolic products that may render them unpalatable to some herbivorous fishes. Brown algae contain polyphenolic compounds (tannins) that are known to act as a chemical defence against browsing fishes. Highly calcareous algae may also be unpalatable to some fish species, although girellids have developed a feeding apparatus and a grinding gizzatd that enables rhem to assimilate these algae.

A third explanation for the depauperate herbivorous fish fauna may lie in the limitations on the feeding apparatus of these fishes. It has been argued that most fish are too small to consume enough algae to meet energetic demands. Studies on sea carps, for example, have shown that only large adult fishes can meet enetgetic demands by consuming algae alone. Small fishes can only do this by supplementing theit diet with animal material ot being completely catnivorous as juveniles.

Whatever the teason, understanding why *there are so few types of herbivorous fish on* temperate rocky reefs is unlikely to be a simple stoty. Herbivory has evolved a numbers of times under different circumstances, indicating that there may be many different ways to be a herbivore. There is probably no general role of herbivorous fishes in temperate waters because there is no 'typical' feeding mode. The facet of their biology that makes them most interesting is the diverse means by which each species consumes and assimilates plant material. The biology of herbivorous fishes remains one of the most perplexing and poorly undetstood aspects of temperate rocky-reef ecology.

▽ A patch of Common Kelp that has been recently cleared by female Herring Cale. Note the forest of denuded plants. Sydney, New South Wales. *Neil Andrew*