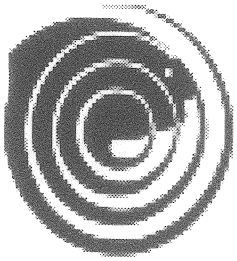

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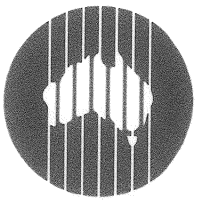

CSIRO MARINE RESEARCH

DEVELOPMENT OF A RAPID-ASSESSMENT TECHNIQUE TO DETERMINE BIOLOGICAL INTERACTIONS OF FISHES, AND THEIR ENVIRONMENT, AND THEIR ROLE IN THE ECOSYSTEM

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OBJECTIVES:

1 Measure the functional morphology of 50 species (including quota species) in the SEF shelf trawl fishery, including their internal and external features.

2 Analyse these morphological features to determine the structure of species assemblages, habitat use, and possible biological interactions.

3 Compare the information on community structure, habitat use and biological interactions derived by this study against independent information on habitat use, water column distribution and diet, to determine which morphological features provide useful information on the fishes' ecological role.

4 Ascertain the potential of functional morphology to rapidly and efficiently provide the information on species interactions, habitat use and susceptibility to fishing gears that is essential to fishery management based on ESD principles.

5 **Derived objective:** to develop an analytical technique for ecomorphological data, typically characterised by 'mixed attributes'.

NON-TECHNICAL SUMMARY

For many years, scientists have observed large open marine ecosystems from the viewpoint of a fisher. Fish and, less frequently, other bottom creatures are first seen when they are brought to the surface in nets, lines or baskets. A scientist onboard a fishing vessel aggregates these collections over the catching area of the gear. If the fish are not seen until they reach the market, they are aggregated over the area fished by the vessel, fishing fleet, or the entire fishery. Data the numbers, sizes and ages of fishes in the catch have been the traditional basis of fisheries management, and much effort has been spent on developing concepts and techniques for managing individual species.

However, no species exist in a vacuum – they are affected by their habitat, environment, predators and prey. Since the 1920s, starting with A.J. Lotka and Vito Volterra, scientists have been developing ideas and models to explore the interactions of species. The earliest models were homogenous in respect to space and time – most still are (see Bax 1999 for review). Lotka, in fact, used an analogy between biological populations and homogenous chemical

systems. At the same time, fishery scientists had mainly dead fish from aggregated catches to work with. The stomachs of dead fish were analysed to determine who eats whom, and predator-prey interactions became the grist of multispecies modelling in the marine realm. For the lack of anything better, multispecies modelling remains the basis of – and is often considered synonymous with – ecosystem management.

In recent decades, scientists have developed the tools to look under the ocean surface, and have discovered what most fishers know: the system is anything but homogenous. At the same time, the difficulty of describing multispecies interactions largely through predation, except in very rare circumstances, has become better appreciated (e.g. Beverton 1985). Releasing marine science from the assumptions of homogeneity has, however, resulted in confusion as to how to describe and understand marine ecosystems. "Inability to deal with the complexity of the spatio-temporal framework of ecological systems is one of the underlying causes of the current ambiguity in the ecosystem concept" (O'Neill *et al.* 1986, p. 30). Recognition of this ambiguity in the ecosystem concept has coincided with a greater demand for ecosystem management – legislative requirements are running ahead of scientific understanding.

Protection of biodiversity and habitat are the values on which much of current ecosystem management is based – marine protected areas or multiple-use areas are the commonly suggested tool. However, how a species uses its habitat affects how the habitat and its spatial distribution are defined. This causes major differences in how to value habitat and its spatial characteristics for conservation (Arnold 1995). Additionally, connectivity between habitat depends not only on the abundance and spatial patterning of habitat, but also on the habitat-specificity and dispersal ability of the species. Highly agile species may see the landscape connected across a greater range of fragmentation severity, and there may be threshold levels at which habitat no longer acts as an aggregation device depending on a species characteristics (With and Crist 1995). It is clear that replacing one static view of marine ecosystems – equilibrium-based predator-prey models – with another static view – biodiversity and habitat – is unlikely to provide us with the appropriate information with which to manage these complex dynamic systems.

Australia has already taken the first scientific steps towards managing its marine environment by defining particular marine bioregions, assumed to be functionally independent areas, based on the diversity and richness (i.e. biodiversity) of fish (IMCRA Technical Group 1997). But Australia is committed to not only protecting marine biodiversity, but also ecological processes, and using its marine resources sustainably (IMCRA Technical Group 1997). Can biodiversity highlight important ecological processes? What is the relationship between biodiversity and sustainability? And where within each bioregion would a protected area, or system of protected areas, be placed, and how would this decision be made?

Clearly a rapid method of defining ecologically meaningful areas within bioregions and linking biodiversity to ecological processes is urgently needed. The need is nowhere greater than the southeast of Australia where, under Oceans Policy, Australia's first regional management plan is to be implemented in the next few years. If such a plan is to provide benefits to users of this area – including the fishers of the South East Fishery – it is clear that it must be based on the best available information.

In this project we have attempted to develop a classification of the fish component of the southeast Australia shelf ecosystem that is based not on species, but directly on ecological

processes. In this way we hope to describe the relationship between fish communities, ecological processes and sustainability (at the system level) more clearly than could be done by assessing species abundance or biodiversity. By integrating the data on a level higher than individual species we also have attempted to develop a rapid assessment technique that can be applied to assess fish communities and their ecological role in the absence of detailed taxonomic, habitat and dietary data.

Ecomorphotypes, for the southeast Australian shelf ecosystem, were developed through aggregating species into distinct functional groups based on their morphological adaptation to locomotion, feeding and self-preservation – although self-preservation was not found to be a very useful axis for aggregation, as some important characters were not measured. Each ecomorphotype contained from 1 to 23 species, which would be an underestimate, as we categorised only 114 species out of ~230 caught during the SEFEHS project (FRDC Project 94/040), a total of 411 species are considered as likely to live in the study area. The final 20 ecomorphotypes represent unique combinations of the locomotion, feeding and aspects of the self-preservation functional groups (out of a possible 75). These ecomorphotypes are quite stable:

- They bear considerable resemblance to the morphotypes described through aggregating the entire dataset;
- They can be recovered from a reduced dataset (21 measurements and 18 coded characters)
- The ecomorphotypes can be named – i.e. they represent groups with distinct ecological characteristics.

Furthermore, the community structures, based on ecomorphotypes, demonstrate a striking similarity between the northern and southern regions of the study area (representing the Central Eastern and the Bassian and Tasmanian provinces within the biotone, respectively). This is especially illustrative of the power of the ecomorphotype analysis. Whereas the IMCRA Bioregion Analysis detected a difference between these two provinces based only on taxonomy (with associated importance for biodiversity), ecomorphotype analysis shows the similarity in the community structures of the regions (with associated importance for ecological processes and sustainability).

"Like elephants, ecosystems can be viewed from many perspectives. Our conclusions are biased by the way we observe ecosystems." (O'Neill *et al.* 1985, p. 3). There is no one best way to view an ecosystem. Ecosystems contain structural constraints that operate on organisms and functional constraints that act on processes, and the two cannot be considered separately without introducing significant ambiguity. Ecomorphology is one approach that links structure and function. It provides a new perspective on the fish community of the Southeast Australian continental shelf that can be used in determining the appropriate shape and scale of ecosystem management.

KEYWORDS: **rapid assessment, ecomorphology, Australian southeast fishery, functional groups, ecosystem structure, morphology**

1 BACKGROUND

> "[There is] a certain Chinese encyclopedia in which it is written that:
> 'animals are divided into: a) belonging to the emperor, b) embalmed, c) tame, d) sucking pigs, e) sirens, f) fabulous, g) stray dogs, h) included in the present classification, i) frenzied, j) inumerable, k) drawn with a very fine camel hair brush, l) et cetera, m) having just broken the water pitcher, n) that from a long way off look like flies'.
> The wonderment of this taxonomy, the thing we apprehend in one great leap . . . as the exotic charm of another system of thought, is a limitation of our own . . . the stark impossibility of thinking that".
> (Foucalt, M. 1973. The Order of Things)

The need to manage fisheries in the context of their environment is increasing. This requires a better understanding of the link between the fishery and the ecosystem. The studies to provide this understanding – food web, fish community identification and ecosystem (SEF Draft Strategic Research Plan) – are extensive (and expensive). For example, ICES researchers analysed fish stomach contents to model the biological interactions of the five main commercial species in the North Sea. In 1981 they analysed 55,166 stomachs; in 1991, 92,894 (and in 1981 sampling they omitted five non-commercial species later found to prey heavily on commercial species). Nevertheless, their studies indicated that a proposed increase in mesh size would be counterproductive for the fisheries, since smaller fish, which would escape the larger mesh, are significant predators on the juveniles of important commercial species.

Understanding the biological structure of marine fisheries and fishery ecosystems, and the way they interact, is fundamental to managing them. The way to achieve this understanding is not so clear. The multinational effort required for the North Sea study is beyond the scope of Australian fisheries, with their greater biological diversity and smaller resource base. An alternative means is required to understand the fisheries ecosystem and to meet management obligations under Ecologically Sustainable Development (ESD).

Marine Biorap (Ward *et al.* 1998) is such a technique; it is designed for the identification and assessment of priority areas of marine biodiversity in less than 18 months. It is also a decision-support tool for implementing marine protected areas (MPA) and managing fisheries outside the MPAs. Biorap uses a stepwise technique of mapping biological and environmental attributes separately, followed by a matching of the two data sets to derive a database of estimated (modelled) distribution patterns of biological elements (*sensu* Ward *et al.* 1998). In most applications of this technique, surrogates for marine biodiversity will need to be chosen, to represent a range of structural and functional elements. Typical choices of structural process surrogates are species, genera and families, but also assemblages and habitats; functional process surrogates are typically recruitment processes and life-history strategies (Ward *et al.* 1998).

Biorap is focused on biodiversity and its conservation, relying on species or higher taxon information for identifying priority areas. However, in recent discussions of community management, the emphasis has shifted away from phylogenetic towards functional groups (Bahr 1982; Barbosa and Galdean 1997; Grime 1997). It is becoming apparent that ecosystems cannot be managed purely for species diversity because "the functional characteristics of the component species in any ecosystem are likely to be at least as important as the number of

species for maintaining critical ecosystem processes and services" (Hooper and Vitousek 1997).

Habitat loss and practices that change functional diversity and functional composition are likely to have large impacts on ecosystem processes (Tilman *et al.* 1997). As there is continued loss in biodiversity and genetic diversity worldwide, it is critical that we develop a recognition of what is most important to preserve, and whether current losses are sufficient to impair ecosystem functioning – with all the problems that brings. A review in *Science* concluded that the most immediate problem is to identify irreplaceable species and functional types (Grime 1997). It is necessary to progress from the long-standing theoretical arguments over whether higher diversity leads to more or less system stability, and to "reassert a more Darwinian perspective in which high species-richness is viewed not as an attribute of certain ecosystems but instead as a function of population processes associated with special circumstances that hover precariously between two different forces for extinction (extreme habitat conditions and competitive dominance)" (Grime 1997).

Functional groups of species may be defined on the basis of habitat, trophic position, life style, size or other characteristics (Bahr 1982); combined, the groups more accurately reflect changes in the environment or fishery than would the individual species. Possibly such species groups (or guilds) reflect the characteristics of a higher ecological unit than species – a unit that responds to environmental change more predictably than do individual species (Austen *et al.* 1994). Bahr (1982) argues that, for ecological studies, a functional taxonomy is needed, to parallel the traditional, phylogenetically based classification scheme. He loosely bases his functional taxonomy on the guild as defined by Root (1967): "a group of species that exploit the same class of environmental resources in a similar way". However, in order to view a community in terms of functional groups, its interactions have to be well understood – and that means either expensive ecosystem studies or alternative techniques.

This project was designed to develop and test a method for rapidly assessing community structure, defining species groups (based on functionality) and biological interactions in marine ecosystems, by capitalising on the existing Southeast Fishery Ecosystem Habitat Study, SEFEHS (FRDC Project 94/040; Bax and Williams 1999). The study area of this project – a part of the Australian Southeast Self Fishery – is contained in the South Eastern Biotone, a zone of faunal overlap, strongly dominated by warm, temperate elements of the Central Eastern Province, but also influenced by the cool, temperate Bassian and Tasmanian, as well as by the tropical North Eastern, provinces (Fig. 1.1.1, IMCRA Technical Group 1997). Hence, the temperate shelf ecosystem in this area is characterised by high biological diversity not just at the species level, but also at higher levels. This diversity provides a database of high contrast, increasing the probability that this technique will succeed in delineating ecological groups that are relevant to, and can simplify, fisheries management and ESD. Furthermore, the SEFEHS (FRDC Project 94/040) provides a description of the predatory interactions, habitat use, and resource overlap of 50 or more of the common shelf species, together with the biological, spatial and to some extent physical structure of this shelf fishery ecosystem. It thus provides data to assess the validity of the functional groups, defined in this project.

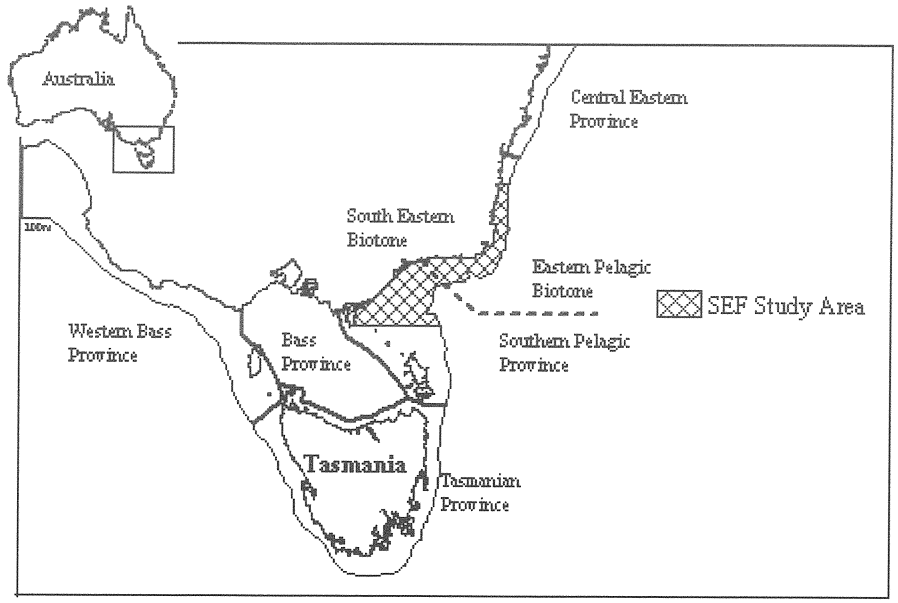


Figure 1.1 Location of the South East Fishery Project study area (hatched) in relation to the demersal (solid lines) and the pelagic (dashed line) biotones and provinces identified in IMCRA (IMCRA Technical Group 1997)

1.1 The development of a potential rapid assessment technique

A major tenet of ecology is that fish and other species adapt to their environment (or are limited by past evolutionary adaptions to the environments they can inhabit). It has led to the development of a principal field in ecology: ecological morphology or ecomorphology – the study of the interaction of morphological and ecological diversity.

The field of ecomorphology has a long history; the theory was first developed in *On the Origin of Species* (Darwin, 1859). The more recent interest in ecomorphology came as ecologists realised that the morphology of an organism is a clue to answering questions its about niche, competitors, community structure and morphological variations among individuals or among species (Motta *et al.* 1995a). Furthermore, ecomorphology can be used to detect and explain convergent evolution (Karr and James 1975). A key observation of ecomorphology is the that morphological variation among individuals or among species can vary performance and, ultimately, resource use and evolutionary fitness (Wainwright 1994).

One of the purported advantages of ecomorphology is its predictive power (Smirnov *et al.* 1995, Motta *et al.* 1995b, Sibbing *et al.* 1994). Once a direct link between function and form is established by ecomorphological analysis, specific functional and structural demands on the organism can be formulated from its ecological niche; or, vice versa, environmental constraints and potential can be predicted for specific structures of an organism (Sibbing *et al.* 1994). Recent examples are the ecomorphological correlates of 10 distantly related species of seagrass fishes being used to predict their microhabitat (Motta *et al.* 1995a), or the habitat of 34 species of Caribbean reef fishes being used to predict their diet (Wainwright and Richard 1995). Also, Sibbing *et al.* (1994) successfully used ecomorphology in the developing fishery of Lake Tana

(Ethiopia) to deduce from their feeding structures the abilities and limitations of various fish types to exploit the resources. A subsequent diet and distribution study confirmed that the identified morphotypes occupied different food-niches and preferred different depths and substrates (Nagelkerke *et al.* 1994).

It is this predictive power of ecomorphology we propose to harness. As mentioned in the previous section, Marine Biorap uses structural and functional process surrogates that rely heavily on species and higher taxa but also on assemblages, habitats, recruitment processes and life-history strategies (Ward *et al.* 1998). Ecomorphology has the potential to incorporate a combination of these surrogates into a few simple measures. Furthermore, it distinguishes communities based on functional groups rather than on biodiversity; such a distinction, as the previous section implies, is becoming more important to management (Bahr 1982; Folke *et al.* 1996; Barbosa and Galdean 1997; Grime 1997).

1.2 A new approach to analysing ecomorphology data

Data collected for ecomorphological studies have fundamental attributes that severely restrict options for statistically-appropriate analysis. The attributes include: the mixed form of the data; information in missing characters; variables that depend on another variable; and the independence of species as sample units. The particular constraints that these data attributes cause in the analysis of ecomorphology data were identified half a decade ago. It is thus surprising to see that many recent and contemporary studies have not taken them into account. In the present study we describe a novel approach to treating hierarchical and mixed-attribute data and the associated analytical problems. We then apply it to analysing a suite of temperate marine fishes.

Morphometric data usually include counts and coded descriptors for shapes and positions of structures (e.g. Gatz 1979b; Motta *et al.* 1995a; Labropoulou and Eleftheriou 1997; Piet 1998) in addition to metric measurements. Because integers and numeric codes do not behave the same way mathematically as continuous, metric data (*sensu* Belbin 1994), caution is needed in applying standard analytical techniques to mixed-attribute data. There are similar problems with combining measurements and ratios of measurements (Miles and Ricklefs 1984), and/or measurements with different scales (e.g. Karr and James 1975) in single analyses.

Another statistical difficulty is that many morphological measurements are dependent on the presence or absence of a particular structure: for example the shape of a fin can be recorded only if the fin is present in the first place. Gower (1971) views this type of data hierarchically, with presence/absence being the primary character and any subsequent measures being secondary. Since most ecomorphology studies concentrate on closely related species (e.g. Norton 1995; Foster and Baker 1995), hierarchical characters may not pose a problem, as correspondence in primary characters among related species is high. Still, considering the taxonomic spread of the present study this issue needed to be addressed.

Last, but not least, Felsenstein (1985) points out the problem of phylogeny when using species as statistical samples. Species, due to their evolutionary relatedness, are inherently non-independent. But even robust, non-parametric statistical methods can rarely cope with non-independence of samples – unless they are specifically designed for it. Felsenstein (1985)

proposes the use of cladistic evolutionary trees with known divergence distances to correct for the non-independence.

In addition to the form of the data, the ordination used for the analysis needed some closer attention. Minchin (1987) noted that linear ordination methods are often inappropriately used for analysing gradients in ecological data, because the data is non-linear in nature. This is the case in many ecomorphological studies where principal component analysis (PCA) and canonical correlation analysis (CCA) – both linear ordination techniques – are most frequently used (e.g. Karr and James 1975; Norton 1995; Winemiller 1991; Piet 1998).

New techniques are developed in this study to develop similarity measures appropriate to the attributes of the data collected in studies of ecomorphology. These similarity measures are analysed by non-linear ordination techniques.

1.3 Direct use of results of applying ecomorphology to the Southeast Fishery

The main goal of this project was to develop a technique that could be used to quickly and effectively describe the primary features of community structure in relation to habitat use and biological interactions of fish species in Australia's fished ecosystems. This would provide information to fisheries managers, enabling them to determine indirect biological interactions that could reverse or nullify management interventions.

There is no guarantee that this goal can be attained. Some ecomorphology studies have not accurately predicted predation interactions (e.g. Motta *et al.* 1995a), although this may be due to their not analysing environmental and morphological correlates jointly, particularly to account for variation between microhabitats (Wainwright and Richard 1995). Despite considerable research in this area , there is as yet no consensus on the predictive power of morphology in ecology (Wainwright 1994). However, even if this goal is not attained, this project will have three direct benefits to the Southeast Fishery (SEF):

1 It will provide a highly informative model of biological interactions in this fishery, which could be used in the SEFEHS study to interpret the collected data, particularly in trophodynamic models

2 It will collect basic biological information on the fishes in the SEF (such as length-girth and length-gape relationships) that may be used to determine the selectivity of alternative sampling gears,

3 It will provide a database of biological information on the fishes of the SEF that can be used to estimate target strength for identifying species in acoustic surveys and will have further uses in future biological and impact studies of the SEF.

2 NEED

The Problem

Industry and managers in the SEF face increasing legislative pressure, as well as pressure from other interest groups to demonstrate that the fishery is ecologically sustainable. Furthermore, as a first step in Australia's comprehensive Oceans Policy, the south-east marine domain has been selected as the first region for multi-use, ecosystem-based regional marine planning. A key issue in managing the region and demonstrating the fishery's sustainability is understanding the relative roles of natural processes and human impacts - with imperfect knowledge of either.

In particular, there are several changes in the SEF that have the potential to modify fishing impacts on the system:

- Continuing increases in overall effort
- Shifts in the effort of commercial fisheries, between areas and sectors
- Increased targeting of 'hard grounds'
- Modifications to vessels, navigational equipment and fishing gear
- Markets and quota holdings

A Solution

This project proposes to develop an ecological tool to cost-effectively define species interactions, community structure and habitat association. This will further our understanding of the temperate shelf ecosystem.

The project builds on an existing FRDC-funded project of the SEF shelf habitat ecosystem (FRDC Project 94/040) and will provide a logical framework in which to assess interactions between species and their use of habitat in the SEF. The project uses the existing extensive biological data on, and samples from the SEF shelf ecosystem. These data and samples provided a unique opportunity to develop our understanding of the SEF ecosystem and to show the potential value of this method to all Australian fisheries.

3 OBJECTIVES

There were four original objectives for this project. Once we started analysis of the collected data, it became clear that available analytic techniques were inadequate (actually incorrect). This necessitated our adding a fifth objective.

1 Measure the functional morphology of 50 species (including quota species) in the SEF shelf trawl fishery, including their internal and external features.

2 Analyse these morphological features to determine the structure of species assemblages, habitat use, and possible biological interactions.

3 Compare the information on community structure, habitat use and biological interactions derived by this study against independent information on habitat use, water column distribution and diet, to determine which morphological features provide useful information on the fishes' ecological role.

4 Ascertain the potential of functional morphology to rapidly and efficiently provide the information on species interactions, habitat use, and susceptibility to fishing gears, that is essential to fishery management using ESD principles.

5 **Derived objective:** to develop an analytical technique for ecomorphological data typically characterised by 'mixed attributes'.

4 METHODS

4.1 Sampling

4.1.1 Location

The southeast Australian continental shelf between the latitudes of 36° and 39°S was the focus of this study (Fig. 1.1.1). The shelf is defined as the area from the coast out to ~170-200 m depth and is 25-km wide in the north of the study area and over 175-km wide in the south. Several small rivers flow into the study area, but Australia being a dry continent, their discharge is minimal. The area has a complex and variable oceanography – eddy fields from the seasonally variable southward flowing East Australian Current follow the shelf break where there is also a northward countercurrent and intrusions of continental slope water (Tranter *et al.* 1982). Summer upwellings occur almost annually under the influence of north easterly winds (Edwards 1990). The southeast Australian continental shelf can be characterised as a moderate to high-energy, wave-dominated environment with autochthonous sediments.

According to a regionalisation of Australia based on the demersal fish fauna (IMCRA Technical Group. 1997), the study area lies within the South Eastern Biotone (SEB), a zone between the Central Eastern Province to the north, and the Bassian and Tasmanian Provinces to the south-west (Fig. 1.1.1). This is a unique transition zone of faunal overlap, strongly dominated by warm temperate elements of the Central Eastern Province, and to a lesser extent by elements of the tropical North Eastern, and the cool temperate Bassian and Tasmanian Provinces. There is a major disjunction at Cape Howe and the extent of southward penetration by northern species appears to be determined by the water masses of the extension of the warm East Australian Current. In addition, the study area is at the eastern boundary of the Southern Pelagic Province, and extends into the Eastern Pelagic Biotone (the transitional zone between the Northern and Southern Pelagic Provinces) – regions distinguished by pelagic fish faunas (IMCRA Technical Group. 1997).

Because our study area lies within a provincial biotone – by definition a zone of overlap between distinct provinces, we were able to test the power of ecomorphology to detect patterns in ecomorphotype groups in relation to provincial structure.

4.1.2 Strategy

Our target species were selected from the ~230 species caught during a five year study of the fishery ecosystem of the same area (the 'SEFEHS' study; Bax and Williams 1999). For the sampling a variety of demersal fishing gears were used – demersal trawl, variable-mesh gillnets, fish traps and a benthic sled, fishing in a range of habitats and therefore catching a wide variety of species and morphotypes. The relatively short duration of the current project (1 year) restricted us to sampling a subset of species for ecomorphological analysis. The choice of species was based on their importance in a number of categories:

- commercial importance
- overall abundance
- biogeographic affinity – the general north/south contrast provided by representative species of families from the Central Eastern and Bassian and Tasmanian provinces
- multiple species from diverse (species-rich) families (to test for the power of the statistical analyses to discriminate function from phylogeny)

One hundred and fourteen fish species, in 53 families (Table 4.1.2.1 and Figure 4.1.2.1) were analysed. Four or more species were collected for 5 primary, and an additional 4 diverse families: Zeidae, Triglidae, Platycephalidae, Carangidae and Monacanthidae (primary); Scyliorhinidae, Rajidae, Urolophidae, Labridae(additional). One representative member for each of the remaining families was considered sufficient.

Table 4.1.2.1 List of study species showing the CAAB code, the abbreviations used in this study and the number of specimens examined

ABREV.	CAAB CODE	FAMILY	SPECIES	COMMON NAME	N
Cela	15001	Scyliorhinidae	*Cephaloscyllium laticeps*	Draughtboard Shark	10
CesA	15013	Scyliorhinidae	*Cephaloscyllium sp. A*	Whitefin Swellshark	1
AssD	15024	Scyliorhinidae	*Asymbolus sp. D*	Orange Spotted Catshark	9
Asan	15027	Scyliorhinidae	*Asymbolus analis*	Grey Spotted Catshark	10
Muan	17001	Triakidae	*Mustelus antarcticus*	Gummy Shark	2
Spzy	19004	Sphyrnidae	*Sphyrna zygaena*	Smooth Hammerhead	1
Sqme	20006	Squalidae	*Squalus megalops*	Piked Spurdog	12
Prnu	23001	Pristiophoridae	*Pristiophorus nudipinnis*	Southern Sawshark	2
Prci	23002	Pristiophoridae	*Pristiophorus cirratus*	Common Sawshark	1
Sqau	24001	Squatinidae	*Squatina australis*	Australian Angel Shark	3
Trfa	27002	Rhinobatidae	*Trygonorhina fasciata*	Southern Fiddler Ray	2
TrsA	27006	Rhinobatidae	*Trygonorhina sp. A*	Eastern Fiddler Ray	1
Hymo	28001	Torpedinidae	*Hypnos monopterygium*	Coffin Ray	1
Nata	28002	Narcinidae	*Narcine tasmaniensis*	Tasmanian Numbfish	9
Raau	31002	Rajidae	*Raja australis*	Sydney Skate	5
RasA	31005	Rajidae	*Raja sp. A*	Longnose Skate	7
Rawi	31006	Rajidae	*Raja whitleyi*	Melbourne Skate	1
Pani	31009	Rajidae	*Pavoraja nitida*	Peacock Skate	1
Urbu	38001	Urolophidae	*Urolophus bucculentus*	Sandyback Stingaree	10
Urcr	38002	Urolophidae	*Urolophus cruciatus*	Banded Stingaree	12
Urpa	38004	Urolophidae	*Urolophus paucimaculatus*	Sparsely-Spotted Stingaree	10
Urvi	38007	Urolophidae	*Urolophus viridis*	Greenback Stingaree	10
TrsB	38014	Urolophidae	*Trygonoptera sp. B*	Eastern Shovelnose Stingaree	3
UrsA	38018	Urolophidae	*Urolophus sp. A*	Kapala Stingaree	5
Cami	43001	Callorhynchidae	*Callorhinchus milii*	Elephantfish	2
Gypa	60006	Muraenidae	*Gymnothorax parsinus*	Green Moray	1
Aupu	117001	Aulopodidae	*Aulopus purpurissatus*	Sergeant Baker	2

ABREV.	CAAB CODE	FAMILY	SPECIES	COMMON NAME	N
Chni	120001	Chlorophthalmidae	*Chlorophthalmus nigripinnis*	Cucumber Fish	12
Gogr	141001	Gonorynchidae	*Gonorynchus greyi*	Beaked Salmon	1
Brs2	209005	Brachionichthydae	*Brachionichthys sp.2*	Australian Handfish	9
Psba	224003	Moridae	*Pseudophycis barbata*	Bearded Rock Cod	7
Lorh	224005	Moridae	*Lotella rhacinus*	Largetooth Beardie	1
Psbc	224006	Moridae	*Pseudophycis bacchus*	Red Cod	5
Mano	227001	Merlucciidae	*Macruronus novaezelandiae*	Blue Grenadier	1
Gebl	228002	Ophidiidae	*Genypterus blacodes*	Pink Ling	12
Caau	232001	Macrouridae	*Caelorinchus australis*	Southern Whiptail	10
Pas1	255003	Trachichthyidae	*Parachichthys sp.1*	Sandpaperfish	10
Ceaf	258003	Berycidae	*Centroberyx affinis*	Redfish	12
Cytr	264001	Zeidae	*Cyttus traversi*	King Dory	3
Cyau	264002	Zeidae	*Cyttus australis*	Silver Dory	10
Zene	264003	Zeidae	*Zenopsis nebulosus*	Mirror Dory	12
Zefa	264004	Zeidae	*Zeus faber*	John Dory	11
Cyno	264005	Zeidae	*Cyttus novaezelandiae*	New Zealand Dory	11
Cehu	279001	Macroramphosidae	*Centriscops humerosus*	Banded Bellowsfish	6
Masc	279002	Macroramphosidae	*Macroramphosus scolopax*	Common Snipefish	12
Hepe	287001	Scorpaenidae	*Helicolenus percoides*	Reef Ocean Perch	12
Nesc	287005	Scorpaenidae	*Neosebastes scorpaenoides*	Ruddy Gurnardperch	8
Heba	287093	Scorpaenidae	*Helicolenus barathri*	Ocean Perch	10
Chku	288001	Triglidae	*Chelidonichthys kumu*	Red Gurnard	9
Leva	288003	Triglidae	*Lepidotrigla vanessa*	Butterfly Gurnard	12
Ptan	288005	Triglidae	*Pterygotrigla andertoni*	Spotted Gurnard	10
Ptpo	288006	Triglidae	*Pterigotrigla polyommata*	Latchet	6
Lemo	288007	Triglidae	*Lepidotrigla modesta*	Minor Gurnard	12
Lemu	288008	Triglidae	*Lepidotrigla mulhalli*	Deep-water Gurnard	12
Sali	288030	Triglidae	*Satyrichthys lingi*	Crocodile Fish	10
Neri	296001	Platycephalidae	*Neoplatycephalus richardsoni*	Tiger Flathead	11
Plba	296003	Platycephalidae	*Platycephalus bassensis*	Sand Flathead	5
Plca	296007	Platycephalidae	*Platycephalus caeruleopunctatus*	Blue-spotted Flathead	5
Neau	296035	Platycephalidae	*Neoplatycephalus aurimaculatus*	Toothey Flathead	8
Pllo	296036	Platycephalidae	*Platycephalus longispinis*	Long-spined Flathead	10
Hoha	297001	Hoplichthydae	*Hoplichthys haswelli*	Deepsea Flathead	12
Lepu	311001	Serranidae	*Lepidoperca pulchella*	Eastern Orange Perch	20
Cale	311002	Serranidae	*Caesioperca lepidoptera*	Butterfly Perch	10

ABREV.	CAAB FAMILY CODE	SPECIES	COMMON NAME	N
Apan	311053 Percichthyidae	*Apogonops anomalus*	Threespine Cardinalfish	12
Sifl	330014 Sillaginidae	*Sillago flindersi*	Eastern School Whiting	8
Trde	337002 Carangidae	*Trachurus declivis*	Jack Mackerel	1
Trno	337003 Carangidae	*Trachurus novaezelandiae*	Yellowtail Horse Mackerel	12
Sela	337006 Carangidae	*Seriola lalandi*	Yellowtail Kingfish	10
Psde	337062 Carangidae	*Pseudocaranx dentex*	White Trevally	1
Trmu	337077 Carangidae	*Trachurus murphyi*	Peruvian Jack Mackerel	10
Emni	345001 Emmelichthyidae	*Emmelichthys nitidus nitidus*	Redbait	10
Pame	349001 Gerreidae	*Parequula melbournensis*	Silverbelly	1
Paau	353001 Sparidae	*Pagrus auratus*	Snapper	8
Pemu	357001 Pempheridae	*Pempheris multiradiata*	Common Bullseye	1
Atst	361010 Scorpididae	*Atypichthys strigatus*	Mado	1
Pala	367002 Pentacerotidae	*Paristiopterus labiosus*	Giant Boarfish	1
Pere	367003 Pentacerotidae	*Pentaceropsis recurvirostris*	Longsnout Boarfish	2
Zael	367005 Pentacerotidae	*Zanclistius elevatus*	Longfinne Boarfish	8
Nedo	377002 Cheilodactylidae	*Nemadactylus douglasi*	Blue Morwong	9
Nema	377003 Cheilodactylidae	*Nemadactylus macropterus*	Jackass Morwong	12
Chsp	377006 Cheilodactylidae	*Cheilodactylus spectabilis*	Banded Morwong	1
Lali	378001 Latrididae	*Latris lineata*	Striped Trumpeter	1
Note	384003 Labridae	*Notolabrus tetricus*	Bluethroat Wrasse	1
Bosp	384035 Labridae	*Bodianus sp.*	Eastern Foxfish	1
Acvi	384043 Labridae	*Achoerodus viridis*	Eastern Blue Groper	1
Bofr	384057 Labridae	*Bodianus frenchii*	Foxfish	1
Boun	384061 Labridae	*Bodianus unimaculatus*	Eastern Blackspot Pigfish	1
Paal	390001 Pinguipedidae	*Parapercis allporti*	Barred Grubfish	7
Gnin	400001 Uranoscopidae	*Gnathagnus innotabilis*	Bulldog Stargazer	1
Kala	400003 Uranoscopidae	*Kathetostoma laeve*	Common Stargazer	1
Kaca	400018 Uranoscopidae	*Kathetostoma canaster*	Speckled Stargazer	10
Syca	427001 Callionymidae	*Synchiropus calauropomus*	Common Stinkfish	12
That	439001 Gempylidae	*Thyrsites atun*	Barracouta	12
Resu	439002 Gempylidae	*Rexea solandri*	Gemfish	5
Scau	441001 Scombridae	*Scomber australasicus*	Blue Mackerel	7
Sebr	445005 Centrolophidae	*Seriolella brama*	Warehou	14
Sepu	445006 Centrolophidae	*Seriolella punctata*	Spotted Trevalla	9
Loga	460001 Bothidae	*Lophonectes gallus*	Crested Flounder	7
Peje	460002 Bothidae	*Pseudorhombus jenynsii*	Smalltooth Flounder	1
Amro	461001 Pleuronectidae	*Ammotretis rostratus*	Longsnout Flounder	5

ABREV.	CAAB CODE	FAMILY	SPECIES	COMMON NAME	N
Avir	465002	Monacanthidae	*Acanthaluteres vittiger*	Toothbrush Leatherjacket	4
Eumo	465003	Monacanthidae	*Eubalichthys mosaicum*	Mosaic Leatherjacket	10
Pasc	465005	Monacanthidae	*Meuschenia scaber*	Velvet Leatherjacket	11
Neay	465006	Monacanthidae	*Nelusetta ayraudi*	Chinaman Leatherjacket	4
Pafi	465024	Monacanthidae	*Paramonacanthus filicauda*	Leatherjacket	1
Mefr	465036	Monacanthidae	*Meuschenia freycineti*	Sixspine Leatherjacket	10
Thde	465037	Monacanthidae	*Thamnoconus degeni*	Degens Leatherjacket	12
Anin	466002	Aracanidae	*Anoplocapros inermis*	Eastern Smooth Boxfish	1
Arau	466003	Aracanidae	*Aracana aurita*	Shaws Cowfish	2
Omar	467002	Tetraodontidae	*Omegophora armilla*	Ringed Toadfish	1
Sppa	467004	Tetraodontidae	*Sphoeroides pachygaster*	Balloon Fish	1
Arfi	467005	Tetraodontidae	*Arothron firmamentum*	Starry Toadfish	1
Dini	469001	Diodontidae	*Diodon nichthemerus*	Globefish	12
Alpi	469002	Diodontidae	*Allomycterus pilatus*	Australian Burrfish	8
		FAMILIES : 53	SPECIES : 114	TOTAL FISH:	743

Two strategies were used for the data collection based on specimen availability and processing time: 5 to 20 fish covering the available size range were taken for 71 species; while, for the remaining 43 species, one specimen, or one of each sex for sexually dimorphic species, was examined. A total of 743 fish were collected, identified, frozen and stored for later examination.

In the laboratory, groups of five to seven fish were defrosted overnight at room temperature (very small fish at 5°C) and, once thawed, kept in a 5°C coolroom; they were processed within a day of thawing. The heads of the processed fish were individually labelled, refrozen and stored at -20°C for possible further analysis.

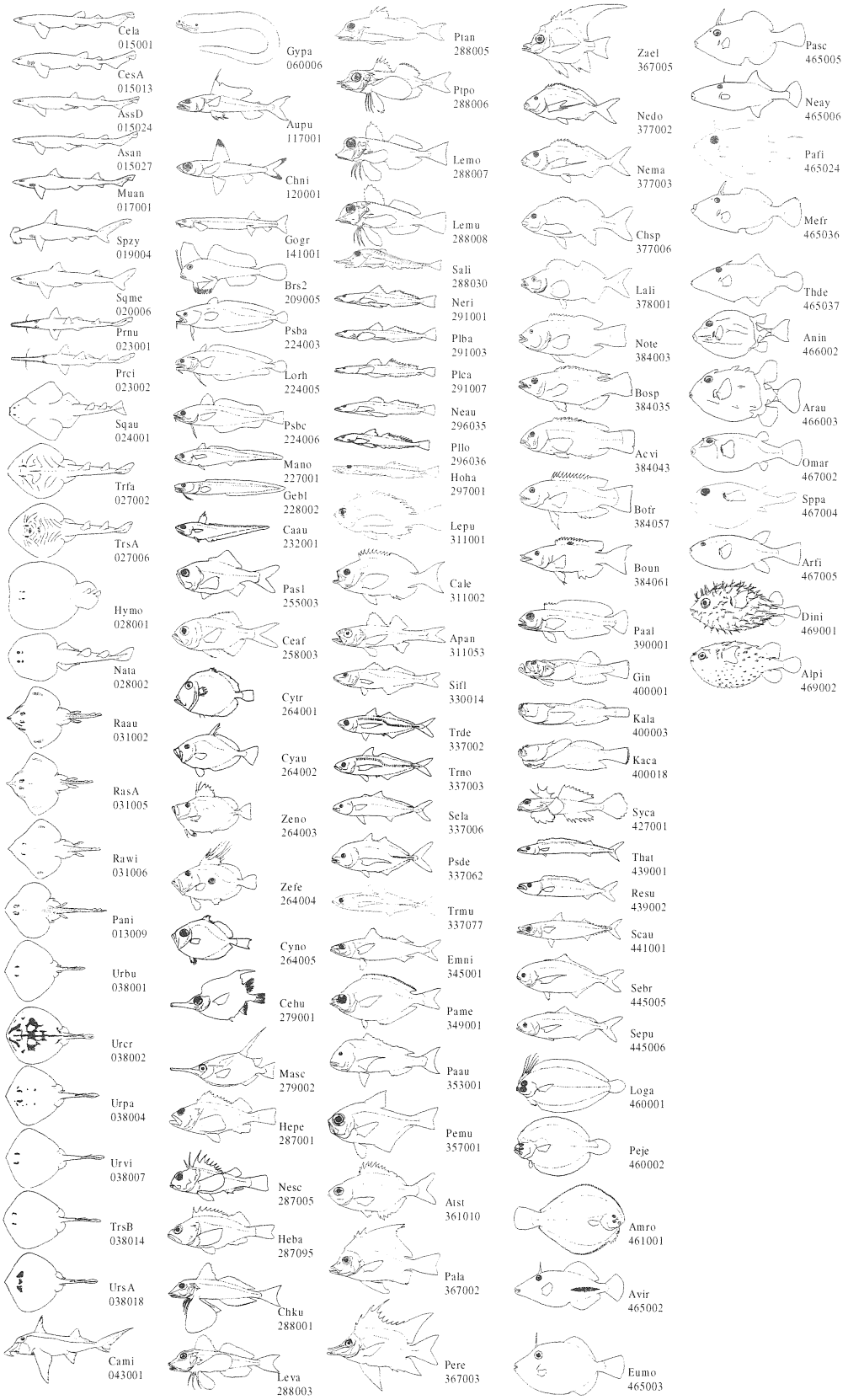


Figure 4.1.2.1 Line drawings of the species included in this study (their respective CAAB code and abreviation are indicated)

4.2 Data collection

4.2.1 Data types

Morphometric studies typically use mixed-attribute data (e.g. Gatz 1979b; Motta *et al.* 1995a; Labropoulou and Eleftheriou 1997; Piet 1998) that need to be treated accordingly in statistical analyses (*sensu* Belbin 1994). Therefore, it is important to identify the data type of each recorded character. Our definition of data types, and the terminology used (Table 4.2.1.1), is based on the two key references used in the development of our analysis - Gower (1971) and Belbin (1994). The data types and their codes are indicated against each of the characters used in our entire character-set.

Table 4.2.1.1 Definition of data types and their coding

DATA TYPES	CODE	DESCRIPTION
CONTINUOUS		
Ratio	1	metric measurements; different values of association for the same differences depending upon the position of the attribute in the range – i.e. the association between 99 and 100 is closer than the association between 1 and 2 (Belbin, 1994)
Interval	2	a series of integers assigned to a character state that reflect a functional ranking (counts are included); the value of the association is not affected by its position in the range (Manhattan distance) (Belbin 1994)
BINARY		
Alternative	3	presence/absence data where joint absences of a character are as relevant as joint presences (Gower, 1971)
Qualitative	4	a series of integers assigned to a character state that do not form an ordered set (e.g. colour); although coded numerically for convenience in computing, in the calculation of a similarity index there are only two levels: match or mismatch (Gower, 1971)
Dichotomous		presence/absence data where joint absences of a character are meaningless (Gower, 1971)
SPECIAL CASES		
Ancillary	5	characters that are unsuited for the general analysis, but may be of interest at a later stage
Redundant	6	characters that are unnecessary for the analysis

4.2.2 Morphological data

Overall, 63 measurements (ratio data) and 139 characters (interval/binary data) were recorded for 114 species (Table 4.2.2.1 and Figures 4.2.2.1 to 4.2.2.7). The weight, sex, gonad stage (Table 4.2.2.2) and the 63 external and internal measurements (data type 1) were taken for each individual. The 139 species-specific characters (e.g. colouration, dentition, shapes and positions of appendices, ie. data types 2-6) were recorded for at least one individual per species, and for one adult specimen (>60% recorded maximum length) of each sex and a juvenile (<30% recorded maximum length) where replicates were available. Norton *et al.* (1995) warned that this type of 'shotgun approach' is likely to swamp potential ecomorphological relationships by

spurious correlations or by phylogenetic influences. He suggested narrowing the list of characters to those that demonstrate some functional relevance. We chose the 'shotgun approach' because we were dealing with a highly diverse fauna and we did not want to restrict the study in the data collection phase. Our reasoning was that the character-set could be reduced but not extended during analysis.

At the end of the data collection phase we realised the potential importance of the red and white muscle distribution in the fillet for determining the burst and sustained swimming potential of the fish. In order to get this additional data we examined the fillet of one new specimen per species, where one was available. Overall, 95 of the 114 species were measured, sexed and their fillets were measured and described following the methods of Yearsly *et al.* (1999).

We measured both traditional taxonomic characters and characters identified in studies of fish function (Alexander 1967; Gosline 1971; Videler 1993; Helfman 1997). This provided the option of selecting the characters of either type that we wanted to include in the analysis (see Section 4.4). Two methods of measuring fish shapes had been employed in previous studies: traditional direct measures based on Hubbs and Lagler (1958) (e.g. Motta *et al.* 1995a, Gatz 1979b; Watson and Balon 1984), and the truss method – a computerised method that produces a systematic geometric characterisation of fish shape using landmarks on the edge of the fish (e.g. Winans 1984; Wood and Bain 1995). Although, Winans (1984) found the truss measurements to be more efficient for stock discrimination purposes, and we did have access to a computer-video link digitising program - MORPHOSYS (Mecham and Duncan 1987), we decided to use the measurements based on traditional methods. Our aim was to develop a rapid assessment technique that may be used in the field, rendering the need for a digitising device impractical. However, we aborted the direct measurement approach standard to taxonomic work, and used horizontal measurements in order to minimise measurement contortions due to varying body depth.

We employed two methods to obtain our ratio data from replicate individuals within a species. Horizontal lengths and areas were measured using MORHOSYS (Mecham and Duncan 1987), a video-link computer program. Widths, depths and internal structures were measured to 0.05 mm using hand-held callipers. All measurements were taken from the left side of the fish, unless the structure to be measured was mutilated on that side; in case of pleuronectiformes the eyed side was measured. Widths and depths were measured on fishes suspended by their eyes to reduce shape distortions.

Special consideration was given to the pleuronectiformes. The adult form of these fish lives lying on its side. We therefore adjusted our view of these fish on a functional basis: the blind side was considered functionally ventral, and the eyed side functionally dorsal. The measurements and characters were defined according to this view (refer to Table 4.2.2.1).

MORPHOSYS (Mecham and Duncan 1987) represented a reliable tool for digitising the chosen landmark points (Figure 4.2.2.1a), automatically projecting them onto the horizontal line defined by the median fork-length (MFL) and measuring the distances. Each fish was pinned on a polystyrene board and landmark points were marked with pins. The board and fish were placed under the video camera and the scale for the current frame determined using a square grid of known size. The points were entered in a predefined sequence and a measurement file created that was later imported into an EXCEL database. Rays were completely hand-measured using corresponding landmark points as indicated in Figure 4.2.2.1b. Fin and body areas (Figures

4.2.2.1a and 4.2.2.1b), as well as gill filament and gill raker areas (Figure 4.2.2.2) were traced onto transparencies using black pen and their area was scanned into the computer and measured. Again, the measurement files produced by this procedure were imported into the EXCEL database.

Species-specific characters (taken from an adult of each sex and a juvenile) were subjectively scored as described in Table 4.2.2.1 and in Figures 4.2.2.3 to 4.2.2.6. Consistency of the recording of character-states was maintained throughout the data collection by only having one observer who was taking meticulous notes of decisions taken on any borderline cases.

Table 4.2.2.1: The measurements and characters used for analysis

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Body	Standard length	Sl	Morphosys measure (h)	1	Horizontal distance from the most anterior part of the snout or upper lip (pt.1) to the caudal base (pt.5) (systematic measurement *sensu* Hubbs and Lagler, 1958) - In sharks the measure was taken to the end of the vertebrae in the tail.- In rays this measurement represents the disk length (measured dorsally)
	Fork length	Mfl	Morphosys measure (h)	1	Horizontal measurement from pt.1 to the centre of the caudal fin (pt.6) (in sharks and rays: total length to the upper lobe of the extended caudal fin)
	Thawed Weight	Wgt	Hand measure	1	Wet-weight of the whole thawed fish
	Abdominal Wall Musculature	Abdom	Qualitative (1-4)	2	Qualitative thickness of the abdominal wall musculature scored from the posterior end of the body cavity:1 thin; 2 moderately thin; 3 moderately thick; 4 thick
	Dermal Filament	Derm_filam	Qualitative (0-1)	5	Presence/absence of dermal filaments
	Luminous Tissue	Lumin_tiss	Qualitative (0-1)	5	Presence/absence of luminous tissue
	Colour Shade Dorsal	Col_dors	Qualitative (1-9)	4 (6)	Main colour-shade of the fish when viewed from above: 1 black; 2 grey; 3 silver; 4 white; 5 brown; 6 green; 7 blue; 8 yellow; 9 red

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Body	Colour Shade Ventral	Col_vent	Qualitative (1-9)	4 (6)	Main colour-shade of the fish when viewed from below: 1 black; 2 grey; 3 silver; 4 white; 5 brown; 6 green; 7 blue; 8 yellow; 9 red
	Countershading	Cnt_shd	Qualitative (0-1)	3	Presence/absence of countershading
	Pattern	Bod_pat	Qualitative (0-3)	2	Degree of distinctiveness of colour patterns on the fish: 0 absent; 1 flecks/spots; 2 intermediately patterned; 3 heavily patterned
	Sensory pores	BSP_dev	Qualitative (1-5)	2	Qualitative size of sensory pores on the body: 1 indistinct; 2 small; 3 medium; 4 large; 5 obvious
	Sens. Pore Numbers	BSP_no	Qualitative (0-2)	2	Qualitative indication of the number of sensory pores on the body: 1 few; 2 numerous
	Body area (side view)	Bod_ar	Morphosys measure	5	Area of the side-view contour of the fish, excluding the fins - rays : ventral view of the body excluding the fins
	Special (dorsal body area of pleuronectiformes)	Special	Morphosys measure	5	Area of the dorsal view of pleuronectiformes only
	Body length	Bl	Morphosys measure	1	Horizontal distance between the most distant point of the opercular membrane (pt.3) and the caudal base (pt.5)
	Body width	Bod_wdth	Hand measure	1	Greatest dimension between the right and left side of the body; in rays: disk width behind head (pt.3) measured ventrally; in Body pleuronectiformes: body depth

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Body	Body depth	Bod_dpth	Hand measure	1	Greatest dimension between the dorsal and ventral surface of the body; in pleuronectiformes body width
	Snout-anus	Snt_anus	Morphosys measure (h)	1	Horizontal measurement from pt.1 to the anterior end of the anal opening (pt.4) (in rays measured ventrally)
	Trunk length	Trunk_l	Morphosys measure (h)	1	Horizontal distance between the most distant point of the opercular membrane (pt.3) and the anterior end of the anal opening (pt.4) (in rays measured ventrally)
	Tail length	Tail_l	Morphosys measure (h)	1	Horizontal distance between the anterior end of the anal opening (pt.4) and the endpoint used in the MFL measurement (pt.6) (in rays measured ventrally)
Peduncle	Shape	Ped_shp	Qualitative (1-3)	2	Degree of flattening of the caudal peduncle: 1 round/sub-quadrangular; 2 oval; 3 compressed/depressed
	Peduncle width	Ped_wdth	Hand measure	1	Smallest dimension between the right and left sides of the caudal peduncle; in sharks and rays: width of tail immediately behind the anus; in pleuronectiformes: peduncle depth
	Peduncle depth	Ped_dpth	Hand measure	1	Smallest dimension between the dorsal and ventral sides of the caudal peduncle; in sharks and rays: depth of tail immediately behind the anus; in pleuronectiformes: peduncle width

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Head	Head length	Hl	Morphosys measure (h)	1	Horizontal measurement from pt.1 to the most distant point of the opercular membrane (pt.3) (Hubbs and Lagler, 1958); in sharks and rays: horizontal measurement from pt.1 to the last gill slit (rays measured ventrally)
	Head width	H_wdth	Hand measure	1	Greatest dimension between the right and left side of the head when the opercles are in a normal position; in rays: greatest disk width in front of pt.3, measured ventrally; in pleuronectiformes: head depth
Head	Head depth	H_dpth	Hand measure	1	Greatest dimension between the dorsal and ventral surface of the head; in pleuronectiformes head width
	Barbels	Barbels	Qualitative (0-1)	3	Presence/absence of barbels
	Sensory Pores	HSP_dev	Qualitative (1-5)	2	Qualitative size of sensory pores on the head: 1 indistinct; 2 small; 3 medium; 4 large; 5 obvious
	Sens. Pores Numbers	HSP_no	Qualitative (0-2)	2	Qualitative indication of the number of sensory pores on the head: 1 few; 2 numerous
Eye	Mobility	Eye_mob	Qualitative (1-2)	2	Degree to which the eyeball can be moved/rotated in the eye socket: 1 fixed; 2 mobile
	Standing up	Eye_sup	Qualitative (0-1)	3	Presence/absence of eyes that are elevated from the plane of the head

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Eye	Position	Eye_pos	Qualitative (1-4)	2	Position of the eyes ranging from lateral to dorsal (Figure 4.2.2.4)
	Colour	Eye_col	Qualitative (1-8)	6	Colour of the iris: 1 grey; 2 blue; 3 brown; 4 red; 5 yellow; 6 (off) white; 7 green; 8 black
	Ocular Tentacles	Occ_tent	Qualitative (0-1)	5	Presence/absence of ocular tentacles
	Eye diameter	Eye_diam	Morphosys measure (h)	1	Horizontal diameter of the eye as externally visual (pt.24 and pt.25)
	Pupil diameter	Pup_diam	Morphosys measure (h)	1	Horizontal diameter of the pupil of the fish (pt.26 and pt.27)
Nostrils	Development	Nostril	Qualitative (1-4)	2	Degree of development of the nostrils:1 rudimentary; 2 feeble; 3 moderately developed; 4 well developed
	Division	Nos_div	Qualitative (1-4)	5	Degree of separation of the inhalant and exhalent nostril: 1 single nostril; 2 partly separated; 3 separated; 4 specialised nostrils
	Nasal Tentacles	Nas_tent	Qualitative (0-1)	3	Presence/absence of nasal tentacles
Mouth	Position	Mth_pos	Qualitative (1-6)	2	Position of the mouth ranging from inferior to superior in 6 steps (Figure 4.2.2.3)
	Tubular snout	Tub_snout	Qualitative (0-1)	3	Presence/absence of a tubular snout

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Mouth	Angle	Mth_ang	Qualitative (1-4)	2	The angle of the maxilla in relation to the horizontal axis of the fish: 1 horizontal (0°); 2 oblique (<45°); 3 strongly oblique (>45°); 4 upright (90°)
	Tongue Development	Tng_dev	Qualitative (0-3)	2	The relative size and development of the tongue: 0 absent; 1 small; 2 moderately developed; 3 well developed
	Tongue Shape	Tng_shape	Qualitative (0-4)	6	The shape of the tongue: 1 elongate; 2 triangular; 3 rounded; 4 rectangular
	Oral Cirri	Oral_cirri	Qualitative (0-1)	5	Presence/absence of oral cirri
	Oral Papillae	Oral_papil	Qualitative (0-1)	3	Presence/absence of oral papillae
	Maxilla Extension	Max_ext	Qualitative (1-5)	2	The extension of the maxilla relative to the eye of the fish (Last *et al.* 1983)
	Gape area	Gap_ar	pi * (gape w/2)*(gape h/2)	1	The gape area was computed by the formula: gape_ar = π(wdth/2 x hgth/2)
	Gape width	Gap_wdth	Hand measure	1	Maximum gape width of the fully opened mouth; in pleuronectiformes: gape height
	Gape height	Gap_hgth	Hand measure	1	Maximum gape height of the fully opened mouth; in pleuronectiformes: gape width
	Pharyngeal gape	Pha_ar	Quantitative	1	Diameter of the pharyngeal gape as measured with a graded cone

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Mouth	Premax. protrusion	Pmax_protr	Hand measure	1	Premaxillary protrusability measured from the anterior margin of the head to the posterior margin of the premaxillary on the fully extended mouth (Sutherland 1976)
	Upper jaw L	Up_jaw_l	Morphosys measure (d)	1	Direct measurement from pt. 1 to the end of the maxilla (pt.2); in rays: direct measure from centre of the upper jaw to the corner of the mouth (pt.2' to pt.2)
Lips	Upper jaw	Lip_uj	Qualitative (1-4)	2	Degree of development of the lips of the upper jaw: 1 bony/membranous; 2 moderately developed; 3 well developed; 4 pronounced
	Lower jaw	Lip_lj	Qualitative (1-4)	2	Degree of development of the lips of the lower jaw: 1 bony/membranous; 2 moderately developed; 3 well developed; 4 pronounced
Teeth					The following were recorded for premaxillary, maxillary, dentary, vomerine, palatine, pterygoid, pharyngeal and basiobranchial teeth
	Type	_tp	Qualitative (0-11)	4	Type of tooth: 1 villiform, 2 incisors, 3 conical, 4 canine, 5 molar, 6 cuspid, 7 fused, 8 villiform and canine, 9 villiform and conical, 10 villiform and molar, 11 canine and conical, 12 conical and molar functionally coded into 4 categories: grasping (4, 8, large 3 and 6); holding (1, 9 small 3 and 6); biting (2, 7); crushing (5, 10)

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Teeth	Size Category	_sz	Qualitative (0-6)	2	Size of the teeth
	Special	_dep	Qualitative (0-1)	3	Are the teeth depressible
	No. Rows	_row	Qualitative (0-3)	2	Number of rows of teeth from single row, to few rows (>5), to many rows (<5)
Opercle	Opercle	Opercle	Qualitative (1-3)	2	Rigidity of the opercular cover: 1 rigid/hard bone; 2 flexible/bony; 3 soft/fleshy
Gills	Gill Fusion	Gill_fus	Qualitative (1-3)	2	Degree of closure of the opercular opening and degree of fusion of the gill arches to the opercular cover (Last *et al.* 1983)
	Gill slit opening	Gillslit	Hand measure	1	Direct measurement between the dorsal and the ventral end points of the gill slit opening; in sharks: the first gillslit was measured; in rays: the last gillslit was measured
Gill Rakers	No. Category	Rak_cat	Qualitative (0-5)	2	Number category of the external rakers of the first gill arch: 0 absent; 1 1-10; 2 11-20; 3 21-30; 4 31-40; 5 >40
	Spacing	Rak_sp	Qualitative (1-3)	2	Spacing width of the external rakers of the first gill arch: 1 wide (>2 raker widths); 2 medium (1-2 raker widths); 3 close (<1 raker width)

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Gill Rakers	Flexibility	Rak_flex	Qualitative (1-3)	2	Flexibility of the external rakers of the first gill arch:1 flexible; 2 semi-rigid; 3 rigid
	Type	Rak_tp	Qualitative (1-4)	2	Degree of spination of the external rakers of the first gill arch: 1 smooth; 2 bristles; 3 weak spines; 4 strong spines
	Length	Rak_lon	Qualitative (1-3)	2	Qualitative estimate if the length of the external rakers of the first gill arch: 1 short; 2 medium; 3 long
	Raker L (arch I)	Rak_l_I	Morphosys measure	1	Length of longest external raker of the first gill arch (Figure 4.2.2.2)
Gill Rakers	Raker area swept	Rak_ar	Morphosys measure	1	Sum of the external raker areas (Figure 4.2.2.2) of all the gill arches
Gill Filaments	Spacing	Fil_sp	Qualitative (1-2)	2	Spacing width of the filaments of the first gill arch 1 separated; 2 close
	Flexibility	Fil_flex	Qualitative (1-3)	2	Flexibility of the filaments of the first gill arch: 1 flexible; 2 semi-rigid; 3 rigid
	Length	Fil_lon	Qualitative (1-3)	2	Qualitative estimate if the length of the filaments of the first gill arch: 1 short; 2 medium; 3 long
	Filament L (arch I)	Fil_l_I	Morphosys measure	1	Length of the longest filament of the first gill arch (Figure 4.2.2.2)

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
	Filament area swept	Fil_ar	Morphosys measure	1	Sum of the filament areas (Figure 4.2.2.2) of all the gill arches, the areas of arch I to IV are doubled as these have double rows of filaments; the hemibranch is only measured in sharks and rays
Lateral Line	Development	LL	Qualitative (0-3)	2	Degree of the development of the lateral line: 0 undetectable; 1 present; 2 developed; 3 well developed
	Special	Ll_brnch	Qualitative (0-1)	3	Presence/absence of branching of the lateral line
	Scales	Ll_scl	Qualitative (1-3)	2	Enlargement and type of scales on the lateral line: 1 not enlarged; 2 enlarged; 3 scutes
Scales	Head	Scl_h	Qualitative (0-1)	3	Presence/absence of scales on the head
	Dorsal	Scl_dors	Qualitative (0-1)	3	Presence/absence of scales on the dorsal surface
	Ventral	Scl_vent	Qualitative (0-1)	3	Presence/absence of scales on the ventral surface
	Overlap	Scl_overlp	Qualitative (1-2)	2	Degree of overlap of the scales: 1 weak; 2 high
	Deciduousity	Scl_desc	Qualitative (1-5)	2	Deciduousity of the scales: 1 highly deciduous; 2 moderately deciduous; 3 adherent; 4 strongly adherent; 5 embedded
	Type	Scl_tp	Qualitative (1-5)	6	Type of scales: 1 cycloid; 2 ctenoid; 3 placoid; 4 modified; 5 mixed

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Scales	Form	Scl_form	Qualitative (1-4)	2	Degree of armouring/modification of the scales: 1 flat/normal; 2 raised; 3 spinulated; 4 armoured
	Average Width	Scl_wdth	Average width 1-3	1	The average width of 3 scales of the post opercular area
	Average Height	Scl_hgth	Average height 1-3	1	The average height of 3 scales of the post opercular area
Gut	Total L	Gut_l	Hand measure	1	Total length of the outstretched gut from the pharynx to the anus; if the stomach forms a sack coming off the main path of the gut, it is not included in the measurement
	Pharynx - Pylorus	Pha_pyl	Hand measure	1	Length of the outstretched gut from the pharynx to the insertion of the first pyloric caecum; if the pyloric caeca are absent: to the far end of the stomach (sphincter position).- in sharks and rays: the measurement was taken to the beginning of the spiral valves
	No. Pyloric Caeca	Pyl_caec	Qualitative (0-5)	2	Pyloric caeca count: 0 absent; 1 1-5; 2 6-20; 3 21-50; 4 51-100; 5 >100
	L longest Caecum	Cl	Hand measure	1	Length of the longest pyloric caecum
	Cavity Lining Colour	Cav_line	Qualitative (1-4)	6	Colour of the mesentery lining the body cavity: 1 translucent; 2 silvery white; 3 off white; 4 black
Swim Bladder	Wall	Sb_dev	Qualitative (0-3)	2	Degree of development/thickness of the swim bladder wall: 0 absent; 1 thin/membranous; 2 moderately thick; 3 thick

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Swim Bladder	Special	Sb_spec	Qualitative (0-2)	6	Functionality measure of the swim bladder: 1 gas filled; 2 fat infested
	Volume	Sb_vol	calculated	1	Swim bladder volume was estimated as width squared by length, as the height was often unmeasurable
	Length	Sb_l	Hand measure	1	Maximum length of the swim bladder
	Width	Sb_wdth	Hand measure	1	Maximum width of the swim bladder
	Height	Sb_hgth	Hand measure	1	Maximum height of the swim bladder
Liver	Liver Colour	Liv_col	Qualitative (1-3)	6	Colour of the liver: 1 white; 2 yellow/grey; 3 brown/red
	Liver Weight	Liv_wgt	Hand measure	6	Wet-weight of the whole liver after dissection
Sex	Sex	Sex	Qualitative	6	Sex of the fish: 1 male; 2 female; 3 juvenile or indeterminate
	Gonad stage	Gonad_stg	Qualitative	6 or 5	Maturity stage of the gonads (Table 4.2.2.2)
Fin					The following measurements were taken for spinous and soft dorsal (dssp and dsso), caudal (c), anal (a), pectoral (pc) and pelvic (pv) fins; for pleuronectiformes dorsal and anal fins were defined as functional pectorals, the pectoral fin was defined as dorsal fin, a score of 'absent' was recorded for the anal and pelvic fins

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Fin	Presence	_pres	Qualitative (0-1)	3	Presence/absence of the fin
	Scales	_scl	Qualitative (0-1)	3	Presence/absence of scales on the fin
	Extent of Sheath	_sh	Qualitative (0-3)	2	Extent of a sheath at the base of the fin: 0 absent; 1 short; 2 medium; 3 long
	Rigidity	_rig	Qualitative (1-3)	2	Degree of flexibility of the fin: 1 flexible; 2 semi-rigid; 3 rigid
	Collapsibility	_col	Qualitative (1-3)	2	Degree of collapsibility of the fin: 1 non-collapsible; 2 collapsible; 3 collapsible into a groove
	Area	_ar	Morphosys measure	1	Area of the outstretched fin (Figures 4.2.2.1a and 4.2.2.1b: A1-A6)
	Base	_b	Morphosys measure	1	The base of the fin was measured as the direct distance between the anterior and the posterior insertion points of the fin (Gomon *et al.*, 1994): pts. 7&9, 10&12, 15&17, 18&20, 21&23 respectively – not measured for the caudal fin
	Height	_hgth	Morphosys measure	1	Maximum height of the fin is measured from the anterior point of insertion to the tip (membranous or other) of the anterior lobe (Hubbs and Lagler, 1958): pts. 7&8, 10&11, 13&14, 15$16, 18&19, 21&22 respectively
	Snout-Fin	Snout_	Morphosys measure (h)	1	Horizontal distance between pt.1 and the anterior point of insertion of the fin: pts. 7,10, 15, 18, 21 respectively – not

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
					measured for the caudal fin
Dorsal Fin	Shape (0-9)	Dors_shape	Qualitative (1-9)	4	Description of the shape of the dorsal fin (Gomon *et al.*, 1994): 1 even; 2 slight notch; 3 deep notch; 4 broken continuous; 5 separate, first element single; 6 separate; 7 separate, second element adipose; 8 separate, three portions
Caudal Fin	Shape	C_shp	Qualitative (0-5)	2	Caudal fin shape (Figure 4.2.2.5)
	Span	C_sp	Morphosys measure	1	Direct measurement between the tips of the expanded fin (for rounded fins: vertical measurement over the widest section of the fin)
Pectoral Fin	F Tactile	Pc_tact	Qualitative (0-1)	3	Presence/absence of modifications to the pectoral fin for the reception of tactile stimuli
	F Locomotory	Pc_loc	Qualitative (0-1)	3	Presence/absence of modifications to the pectoral fin for locomotion of the substrate
Pectoral Fin	Span	Pc_sp	Morphosys measure	1	Same measurement as the pectoral fin height (pt.18 to pt.19)
	Position (1-6)	Pc_pos	Qualitative (1-6)	2	Relative hight of the pectoral fin on the side of the fish (Figure 4.2.2.6)
	Angle (1-3)	Pc_ang	Qualitative (1-3)	4	Angle of movement of the pectoral fin in relation to the horizontal axis of the fish: 1 vertical (90°); 2 oblique (acute angle); 3 horizontal (0°)

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
Pectoral Fin	Shape (1-3)	Pc_shape	Qualitative (1-3)	4	Shape of the pectoral fin: 1 falcate; 2 trapezoid; 3 rounded
Pelvic Fin	F Tactile	Pv_tact	Qualitative (0-1)	3	Presence/absence of modifications to the pelvic fin for the reception of tactile stimuli
	Position	Pv_pos	Qualitative (0-3)	2	Position of the pelvic fin in relation to the pectoral fin: 0 absent; 1 jugular; 2 thoracic; 3 abdominal
	Pelvic Base Width	Pv_wdth	Hand measure	1	Width measured between the anterior insertion points (pt.21) of the right and left pelvic fins
Finlet	Presence (0-1)	Finlet	Qualitative (0-1)	3	Presence/absence of finlet(s)
Keel	Development	Keel	Qualitative (0-4)	2	Degree of the development of a keel: 0 absent; 1 weak fleshy; 2 strong fleshy; 3 weak scutes; 4 strong scutes
Muscle/ Fillet	Length	Fit_l	Hand measure	1	Length of the skun, left-side fillet of the fish, measured directly along the dorsal edge
	Depth	Fit_dpth	Hand measure	1	Depth of the skun, left-side fillet of the fish, measured directly across the maximum depth
	Length/Depth ratio	Fit_Ltodpth	Interval (1-3)	2	Length to depth ratio of the skun, left-side fillet; 1 deep (>50%), 2 medium (25-50%); elongate (<25%)
	Thickness	Fit_thick	Hand measure	1	Maximum thickness of the skun, left-side fillet of the fish

Feature	Character	Abbreviation	Measurement Type	Data type	Definition of Measurement (pt.1 to pt.27 refer to landmark points as indicated in Figures 4.2.2.1a and 4.2.2.1b)
	Length to Thickness Ratio	Fit_Ltothick	Ratio of hand measures	1	Length to thickness ratio of the skun, left-side fillet of the fish
Red Muscle	No. of rows	Rm_row	Interval (count)	2	Number of rows of red muscle on the skun, left-side fillet of the fish
					The following were recorded for each of the bands observed
	Continuity of the band	Rm_con	Interval (1-3)	2	Continuity of the red muscle band: 1 continuous, to the end of the fillet; 2 discontinuous, broken or not to the end of the fillet; 3 diffuse, scattered, not a clear line
	Development of the band	Rm_dev	Interval (1-5)	2	Development of the red muscle band: 1 very feeble; 2 feeble; 3 intermediate; 4 pronounced; 5 very pronounced
	Band width	Rm_wdth	Hand measure	1	Width of the main red muscle band
	Band width/fillet depth ratio		Ratio of hand measure	1	Ratio of band width to fillet depth
	Band thickness	Rm_thick	Hand measure	1	Maximum thickness of the red muscle band
	Band thickness/fillet thickness ratio		Ratio of hand measure	1	Ratio of band thickness to fillet thickness

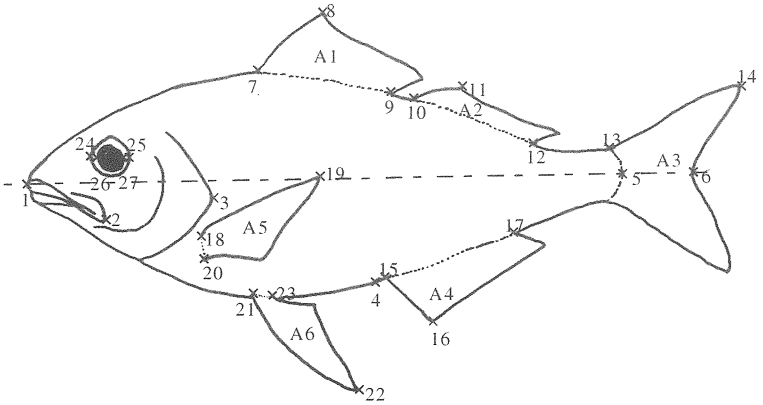


Figure 4.2.2.1.a Landmark points 1-27 and areas A1-A6 for 'Morphosys' measurements on bony fish and sharks, as described in Table 5.2.2.1; for horizontal measurements (h) the landmark points were projected onto the line between pt.1 and pt.5

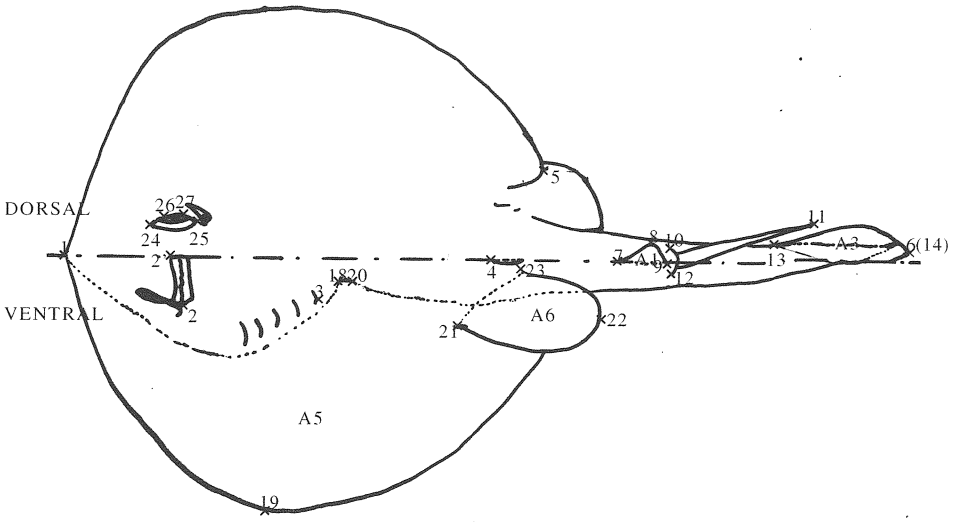


Figure 4.2.2.1.b Landmark points 1-27 and areas A1-A6 (where relevant for 'Morphosys' measurements on rays, as described in Table 5.2.2.1; for horizontal measurements (h) the landmark points were projected onto the horizontal midline

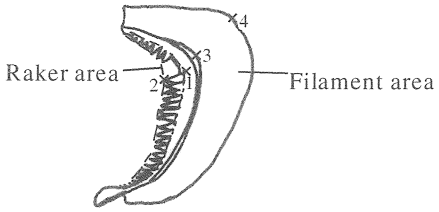


Figure 4.2.2.2 Diagram indicating the gill raker and filament areas as they were measured for 'Morphosys' (raker and filament areas were measured for arches I to VI and for the hemibranch in Chondrichthyes); the landmark points 1-4 for the longest raker and filament were only measured on arch I

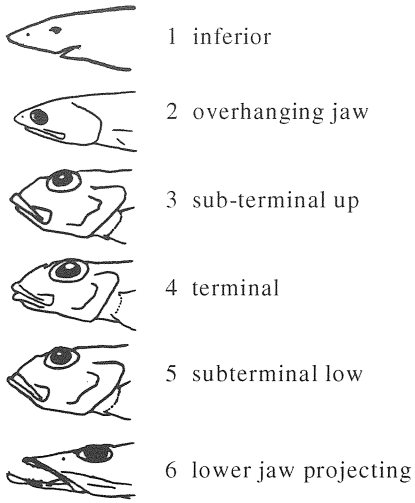


Figure 4.2.2.3 Diagram showing the positions of the mouth as recorded, with their respective name and functional coding

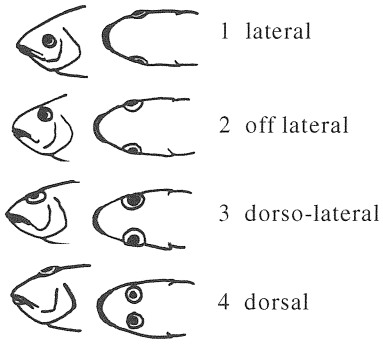


Figure 4.2.2.4 Diagram showing the positions of the eyes as recorded, with their respective name and functional coding

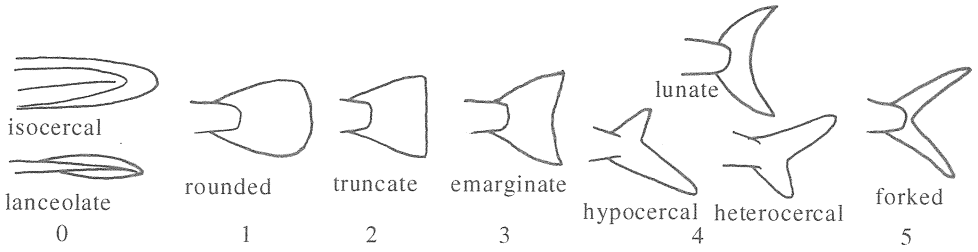


Figure 4.2.2.5 Diagram showing the caudal fin shapes as recorded, with their respective name and functional coding

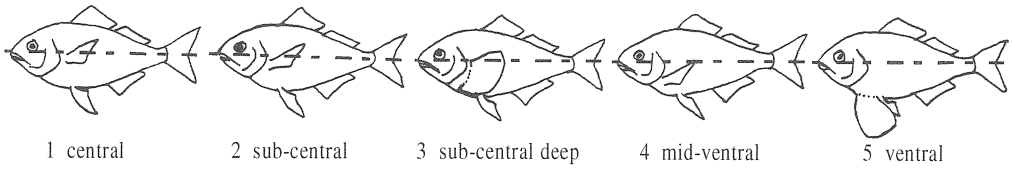


Figure 4.2.2.6 Diagram showing the pectoral fin shapes as recorded, with their respective name and functional coding

Table 4.2.2.2 Generalised macroscopic gonad maturity staging criteria

Stage	Female	Description	Male	Description
1	Immature or virgin	Ovary translucent or indistinguishable	Immature or virgin	Testes thread-like or indistinguishable
2	Resting	Ovary small, light pink or orange oocytes barely visible	Resting	Testes translucent and small
3	Developing	Ovary colour denser, small oocytes visible blood capillaries developing	Developing	Testes opaque and thickening, blood capillaries developing
4	Maturing	Yolky oocytes visible, blood capillaries conspicuous, oocytes not 'loose' in ovary, no hyaline oocytes present	Maturing	Testes large & whitish, milt expressible under pressure, capillaries well developed
5	Mature	Ovaries swollen, bright orange or pink, capillaries engorged, oocytes loose, some hydrated hyaline oocytes visible	Mature/spawning	Testes white & swollen, sperminated; milt flows freely with minimal pressure
6	Spawning	Ovaries swollen with hydrated hyaline oocytes; oocytes flow freely resembling tapioca	Spent	Testes flaccid & bloody, no milt expressible
7	Spent	Ovary flaccid & bloody, residual loose oocytes present, degenerating or resorbing oocytes present	Not applicable	

4.2.3 Ecological data

Ecological data were collected as part of the larger SEFEHS study. Collection methods are fully documented therein. Additional ecological data were collected from the literature where possible. Table 4.2.3.1 summarises the data from the SEFEHS and the literature that were available for interpreting the analyses in this study: the detailed data available may be viewed in the SEFEHS report (Bax and Williams 1999).

Table 4.2.3.1 Summary of Ecological data available from the SEFEHS and Literature

Ecological Data	No. species measured in the SEFEHS	No. species overlapping with ecomorphology	No. ecomorphology species in Literature	No. ecomorphology species with no data available
extreme distribution	N/A	N/A	107	7
extreme depth range	N/A	N/A	107	7
Habitat affinity / assemblage structure	95	67	28 additional	19
Length (max and min)	204 (77 families)	106	107	8
Weight (max and min)	204 (77 families)	106	41	8
Diet	104	67 (59 quantitative)	41	35
Isotope C/N ratio	86	58	N/A	56
max. Age	71 (+8 non-ageable)	54 (+8 non-ageable)	N/A	60
Mortality estimated from max. age	71	54	N/A	60
Fecundity (gonad wgt)	13	11		103

These data were used qualitatively for the interpretation of ecomorphotype groupings. We also used quantitative dietary data (percentage prey- weight) of 53 species, re-grouped on a functional basis into 9 categories (passive and active pelagic invertebrates, fish, cephalopods, armoured and soft mobile benthos, armoured and soft sessile benthos, and infauna) for a principal axis correlation analysis on their feeding ecomorphotypes.

4.3 Statistical Analysis: Morphological data

4.3.1 Data transformation

Missing data

Although, missing data represented a small proportion (<1%) of the whole data set it could not be assumed to be randomly distributed (ref. Tabachnick and Fidell 1983); certain structures were more prone to be damaged and beyond measure than others. In particular the swim bladder and certain fin measurements including MFL were highly susceptible to damage. We had the option of either deleting the species or characters with a high proportion of missing values from our data set, or estimating the missing data points, using a mean or regression (*sensu* Chan and Dunn 1972). The latter approach was used for species where replicate data were available, since these came from a broad size range of individuals. Only 179 of 44580 (ie. 0.4%) ratio data points needed to be estimated.

Problem characters

Swim bladder height and scale measurements had too many missing data to be estimated by regression. The swim bladder measurement was deleted from the data and an approximation of the swim bladder volume was calculated using the length and width of this structure (volume = length x width^2).

The measurement of body scales was problematic, as 'absent' either meant that the scales were highly deciduous and had been lost, or that the scales were too small and too firmly attached to be measured. For this character we decided to transform the ratio data into interval data, scoring them as minute (1), small (2), medium (3), moderately large (4), large (5) or very large (6) depending on their scale area (width x length) to body area (SL x body depth) ratio (1: <0.001, 2: 0.001-0.002, 3: 0.002-0.003, 4: 0.003-0.004, 5: 0.004-0.005, 6: >0.005). For species where no body scale measurements were taken at all, a specimen from the reference collection at CSIRO Hobart was examined for its scale size category.

Size standardisation

Ln-transformation

The ratio data were first adjusted using factors of ten such that the value-range for each character started at 1. Second, they were ln-transformed to reduce the correlation of the measurement means and variances (Winans 1984). Taylor's *b* was computed for a subset of 13 species with 5 or more replicates to assess if ln-transformation was appropriate for our data. The subset of species, chosen to encompass a wide range of overall body size and shape, was the *Cephaloscyllium laticeps*, *Urolophus viridis*, *Genypterus blacodes*, *Zeus faber*, *Helicolenus percoides*, *Lepidotrigla modesta*, *Neoplatycephalus richardsoni*, *Nemadactylus douglasi*, *Kathetostoma canaster*, *Thyrsites atun*, *Seriolella punctata*, *Thamnoconus degeni* and *Diodon nichthemerus*. We concluded that ln-transformation was justified, since the variance of the measured characters within each species scaled proportionally with the square of the mean (*sensu* Bryant 1986).

Principal component analysis (PCA) on logarithmic transformed data may be used in order to accommodate size differences without standardising the data by some common measurement (Green 1979; Bryant 1986, Motta *et al.* 1995a). The size component falls out onto the first PCA axis which can then be excluded from further analyses where size is undesirable. However, PCA is a linear ordination technique and therefore unsuitable for the mixed data types we had collected.

Exploratory analysis was undertaken to establish if multi-dimensional scaling (MDS) removed the size component similarly to PCA. Three-dimensional MDS was performed on a Bray-Curtis similarity matrix obtained from the ln-transformed ratio data for a mixed species subset as well as on a replicate set of pink ling data. This method did not yield any significant results when the scores on MDS dimensions were regressed against SL, even though there is a distinct size factor present, particularly in the case of pink ling (for the analysis refer to Appendix 3). We therefore used a relative measurement approach for separating the size from the shape component.

Relative measurements and indices

The measurements were converted to relative measures using ratios similar to the ones described by Gatz (1979a), Winemiller (1991) and Winemiller *et al.* (1995). These relative measurements are derived by comparing the actual measurement with the body dimension (length, area or volume) and body component (e.g. head, trunk) to which it is most clearly related (Table 4.3.1.1). Some ecologically meaningful indices and ratios defined by Gatz (1979b) and Watson and Balon (1984) were also calculated (Table 4.3.1.1). It was impractical to standardise all measurements to a uniform body size using regression (*sensu* Lavin and McPhail 1985), considering the number of characters that we measured and the large size range of the species examined. Similarly, using a conversion factor derived from the grand mean SL of all fish (*sensu* Adite and Winemiller 1997) was impractical. Packard and Boardman (1987) suggest the use of analysis of covariance (ANCOVA) instead of ratios to increase precision and minimise size effects. In their examples they found that even the standardised ratios of their simulation data were highly correlated with size. Scatter-plots of our relative measurements and indices against SL did not show any particular trend (Appendix 4) satisfying us of the sufficient removal of size effects from the data.

Table 4.3.1.1 Characters and the measurements or indices they were standardised against

Character	Standardisation (division by)
BODY AND HEAD	
Standard length (h)	use in Teleosts for standardisation
median fork length (h)	use in Elasmobranchs for standardisation
Body width	sl (mfl)
Body depth	sl (mfl)
Pelvic base width	bod_wdth
Peduncle width	bod_wdth
Peduncle depth	bod_dpth
Thawed weight	bod_l^3
Liver weight	wgt
Head length (h)	sl (mfl)
Head width	hl
Head depth	hl

Character	Standardisation (division by)
Eye diameter (h)	(bod_l + bod_wdth + bod_dpth) / 3
Pupil diameter (h)	eye_diam
Upper jaw L (d)	hl
Gape width	sl (mfl)
Gape height	sl (mfl)
Gape area (gape_hgt x gape_wdth)	bod_dpth x bod_wdth
Premaxillary protrusion	hL
Gill slit opening	(hL + h_dpth)/2
Compression indices	
Body compression index (BCI)	bod_dpth / bod_wdth
Head compression index (HCI)	h_dpth / h_wdth
Pecduncle compression index (PCI)	pedunc_dpth / ped_wdth
SWIMM BLADDER	
Volume (sb_vol = (sb_wdth)2 x sb_l)	bod_l x bod_wdth x bod_dpth
GUT	
Total L	bod_l
Phar. - pylor.	gut_l
Total caeca length (longest caecum x no. of caecae) (CL)	gut_l
FINS	
Snout_fin (h)	sl (mfl)
Base Length (all direct)	bod_l(all excluding pectoral fin); for pectoral fin: bod_dpth (mfl for sharks)
Maximum Height: element/membrane (all direct)	bod_dpth (only for spinous and soft dorsal and anal fin)
Area (contour)	sl (mfl) x bod_dpth
Fin aspect ratios	
Caudal aspect ratio (CAR = (caud_sp)2 / caud_ar)	------
Pectoral aspect ratio (PAR = (pect_sp)2 / pect_ar)	------
GILLS	
Raker area swept	bod_l x bod_wdth x bod_dpth[a]
Filament area swept	bod_l x bod_wdth x bod_dpth[a]
Gill aspect ratios	
Gill raker aspect ratio (GRAsR)	------
Gill filament aspect ratio (GFAsR)	------

[a] gill raker and filament areas were standardised against a volumetric measurement to account for their physiological relationship with body size.

4.3.2 Similarity indices

Multivariate methods are widely used by ecologists because of their power to detect subtle patterns of differences measured on many variables. Measuring similarity among samples, or groups of samples with respect to the taxa that occur in them is the most common multivariate problem in ecology (Green 1980). Measuring the degree of similarity of two forms is an essential problem in morphometrics (Reyment *et al.* 1984). Ecomorphological studies combine these two, in that the 'samples' (Green 1980)– or 'forms' (Reyment *et al.* 1984) referred to are species and Green's (1980) 'taxa' are replaced by morphological characters. The similarity measure remains as the hinge of the analysis, since any multivariate analysis procedure only reveals the information realised in the resemblance structure (Green 1980). "The conceptual

picture which we form about ecological objects ... is dependent on our perception of their similarities" (Orloci 1978). While choice of a similarity measure can be straightforward for commonly collected data of one type, it is complicated for the mixed attribute data typically collected in ecomorphological studies.

We had to address the problems of mixed attribute data and hierarchical data in the search for a suitable similarity measure for our data. We explored two methods of generating a similarity matrix that appeared to deal with these problems: Gower's (1971) general coefficient of similarity and Belbin's (pers. comment) combined use of separate similarity measures.

Gower's (1971) general coefficient of similarity

Gower (1971) proposed a formula that can accommodate continuous, alternative and dichotomous data:

$$S_{ij} = \sum_{k=1}^{K} s_{ijk} / \sum_{k=1}^{K} \delta_{ijk} \qquad \text{Formula (1)}$$

where: δ_{ijk} signifies the possibility of making a comparison between individuals i and j on the character k; it takes the value one if the comparison is possible, zero if it is not.

s_{ijk} is a score of similarity between individuals i and j on character k; it is zero when i and j are different and a positive fraction or unity when they have some degree of similarity. The scores of s_{ijk} are assigned as follows:

For dichotomous characters presence of character k in i and j results in a score of s_{ijk} = 1 and δ_{ijk} = 1; presence of k in i and absence of it in j, and the vice versa of this, results in a score of s_{ijk} = 0 and δ_{ijk} = 1; and absence of k in both i and j gives a score of s_{ijk} = 0 and δ_{ijk} = 0.

For qualitative characters we set s_{ijk} = 1 and δ_{ijk} = 1 if the two individuals i and j agree in the kth character, s_{ijk} = 0 and δ_{ijk} = 1 if they differ. *Alternative characters* are a special case of qualitative characters where there are only two character states.

For continuous characters (ratio data) with values $x_1, x_2, x_3, \ldots, x_n$ of character k for the total sample of n individuals, $s_{ijk} = 1 - (|x_i - x_j| / R_k)$. Here R_k is the range of character k in the sample. From this follows that s_{ijk} = 1 when $x_i = x_j$ and s_{ik} = 0 when x_i and x_j are at opposite ends of their range. For intermediate values s_{ijk} is a positive fraction.

Furthermore, hierarchical data are weighted in order to accommodate the suite of secondary characters that depend on the presence or absence of a primary character. This is again done using a formula of Gower (1971):

$$S_{ij} = \sum_{k=1}^{K} s_{ijk}(1 + S_{(k)ij}) / \sum_{k=1}^{K} \delta_{ijk}(1 + S_{(k)ij}) \qquad \text{Formula (2)}$$

where: $S_{(k)ij}$ is the similarity between the associated secondary characters of character k. If k_i=k_j=0 or if $S_{(k)ij}$ = 0/0 we define it as $S_{(k)ij}$ = 0

This way of weighting assures that a positive match between primary characters has a higher or equal similarity score to a negative match, which in turn has a higher score than a mismatch on a primary character. Using this formula results in a positive semi-definite similarity matrix that can directly be used in an ordination

But, there is a problem in this hierarchical formula. If the only difference between samples/species is in secondary hierarchical characters, a similarity score of 1 is obtained regardless of matches or mismatches in them. This is a direct result of using the dependent characters to weight the similarity rather than include them more directly into the index (Haskard, CSIRO pers. comment). See Section 5.1 for an example and further discussion.

One could alternatively treat each character equally, with the condition that, if a "primary" character is absent in one of the species, the subsequent comparisons for the "dependent secondary" characters are considered to be impossible, resulting in no score and a δ of zero for these characters. However, this treatment would result in different sets of characters being used to measure similarities between different pairs of species. Importantly, larger character-sets would be used to measure similarities in more closely related species.

For these reasons we looked further for a suitable similarity measure.

Belbin's combined use of separate similarity measures

The two-step system of Austin and Belbin (1982) presented a possible method to accommodate mixed attribute data. Combining (weighted or not) two separate similarity matrices – one for ratio and another for interval data (including alternative data as special case) – allows the use of separate similarity measures appropriate to the respective data type. To account for the problem of hierarchical data, Belbin (pers. comment) suggested weighting interdependent characters according to their numbers. However, strict weighting of a similarity index would result in similar problems as described above, namely including secondary characters only as weighting factor, rather than directly. Furthermore, we found that the two-step system is not suitable for the present situation, as the dataset is composed of ratio and interval data that are hierarchically dependent on one another, a factor that cannot be catered for if the variables are assigned to separate similarity matrices.

Similarity index and weighting technique developed for this study

We combined the ideas of the two approaches described above into a combined similarity index and specialised weighting system. The similarity between hierarchically dependent variables was adjusted, such that a mismatch in a primary character k (always alternative) resulted in a similarity of 0, while a match, be it absent or present in both fish (i and j), resulted in a similarity value between w_p (the weighting given to primary characters) and 1, depending on the number of secondary characters n. If neither i, nor j have a missing (i.e. impossible to record presence or absence) entry in the primary character, the divisor – the possibility of comparing i and j -was set at 1, regardless of missing data in the secondary characters. A weighting value (w_p) of 0.2 was chosen initially as most hierarchical structures in this study contain 5 characters, however, we later examined properties of alternative values. We adjusted the generalised hierarchical Gower (1971) Formula (2) to accommodate hierarchical data as described above (Formula (3)), and used the Gower-Metric similarity measure for

interval/binary data (Formula (4)) and the Canberra Metric similarity measure for the ratio data (Formula (5)). Due to the comparability of the mathematics of these two indices it was not necessary to calculate two separate similarity matrices; the indices could be combined in one mathematical formula:

$$S_{ij} = \frac{1}{K_{ij} + M_{ij}} \left[\sum_{m=1}^{M_{ij}} s_{ijm} + \sum_{k=1}^{K_{ij}} \left(w_p s_{ijk} + \sum_{n_k=1}^{N_k} w_{s(k)} s_{ijn_k} \right) \right]$$

Formula (3)

Where: S_{ij} the similarity between fish i and fish j

s_{ijv} the similarity between fish i and fish j on character v (v can be k (always alternative), n or m);

for interval/binary data s_{ijv} is calculated using the Gower metric index:

$$s_{ijv} = 1 - \left(\left| x_{iv} - x_{jv} \right| / R_v \right)$$ Formula (4)

where: R_v: range of character v

for ratio data s_{ijv} is calculated using the Canberra Metric index:

$$s_{ijv} = 1 - \left(\left| x_{iv} - x_{jv} \right| / \left(x_{iv} + x_{jv} \right) \right)$$ Formula (5)

w_p weighting of the primary hierarchical character, set at 0.2 initially

$w_{s(k)}$ weighting of the secondary hierarchical characters dependent on k:

$$w_{s(k)} = \frac{2 - 2w_p}{N_k}$$

Formula (6)

K_{ij} no. of primary characters (alternative) that are not missing in fish i and/or j

N_k no. of secondary characters dependent on character k

M_{ij} no. of non-hierarchical characters that are not missing in fish i and/or j

Weighting of characters according to their functional importance was not done *a priori* since our analytical strategy (Section 4.4) will take this into account.

Qualitative data, data composed of a series of character states that do not form an ordered set, could not be treated in the same way as ratio or interval data. Belbin (pers. comment) thought that they should be transformed into *alternative data* and then weighted according to how many character states there are for the character in question. On the other hand the same end result could be achieved with less modification by treating such data as qualitative in the way described by Gower (1971) detailed above.

Following test-calculations with different primary character weights (see Section 5.1), we decided to set w_p=0.1 for the present study.

4.3.3 Ordination

Many authors used principal component analysis (PCA) for the analysis of ecomorphological data (Karr and James 1975; Findley and Black 1983; Winans 1984; Watson and Balon 1984; Wikramanayake 1990; Norton 1995 and Motta *et al.* 1995a). The advantage of this approach is that, as mentioned above, the size factor can be eliminated without standardisation and the characters responsible for observed groupings can easily be determined from the factor loadings. While most authors mentioned above only analysed ratio data, Watson and Balon (1984), Wikramanayake (1990) and Motta *et al.* (1995a) used PCA for mixed attribute data similar to ours. Unfortunately, calculating a correlation or covariance matrix – the first step of any PCA – for mixed attribute data violates the assumptions of this analysis (Haskard, CSIRO pers. comment).

Semi-strong hybrid multi-dimensional scaling (SSH) (Belbin, 1994) – a multi-dimensional scaling (MDS) technique that permits combinations of ordinal (monotone), interval or ratio scaling (Belbin, 1994) – was chosen, as it was shown to be a robust technique for the analysis of community data (Minchin 1987). Furthermore, it is not restricted to a particular similarity measure, unlike PCA, allowing for the use of any symmetric semi-positive similarity matrix. Groupings were identified by cluster analysis (flexible UPGMA, Belbin, 1994). Unfortunately, and unlike PCA, a separate analysis is required to relate the original characters to the SSH dimensions and cluster analysis groupings observed. PATN provides two programs for this purpose: principle axis correlation (PCC) and group 'statistics' (GSTA) (Belbin, 1994).

Principal Axis Correlation (PCC)

PCC is a program in the pattern analysis package, PATN (Belbin, 1994) that calculates a multiple-linear regression of individual variables on SSH coordinates. It is designed to show how well a set of intrinsic (used in the ordination analysis) or extrinsic (used only in interpretation of the analysis) attributes can be fitted to an ordination space (Belbin, 1994). PCC analysis results in a set of coordinates of a unit vector in the ordination space for each attribute, as well as the correlations ($|r|$) of these vectors to the SSH coordinates of the samples. By examination of a scatter-plot of the ordination and the PCC it is possible to determine the direction and correlation of best fit and to read off the attributes associated with that direction (*sensu* Belbin, 1994). Basically, PCC allows us, in the present study, to draw meaningful axes into the SSH ordination.

Group 'statistics' (GSTA)

The group statistics program (GSTA) in PATN (Belbin, 1994) compares within-group similarity to between-group similarity. It is thus similar to single factor analysis of variance. It is used to determine the characters causing the splits between groups defined either by a cluster analysis or predetermined and entered manually. GSTA treats ordinal data (ratio and interval) separately from binary data. While it calculates a Kruskal-Wallis statistic (based on an asymptotic approach to the χ^2 distribution) for the prior, it only tabulates percentage of

occurrence for the latter. In order to obtain comparable statistics for both ordinal and binary data, we converted this percentage into a frequency of occurrence and calculated a χ^2. Tests of significance would not be appropriate, but the characters that are most important in differentiating between groups can be identified based on the Kruskal-Wallis and the χ^2 values. This presents a method for character set reduction with retention of the groupings.

We interpreted the group-splits and axis observed in the SSH plot and tested the groups using environmental / biological data using GSTA and PCC.

4.4 Analytical strategy

We required an analytical strategy that used the character-set to identify and discriminate species-groups on the basis of functional rather than phylogenetic relationships. While many of the recorded characters are related to function, others reflect evolutionary history and drive multivariate analyses towards phylogenetic groupings. For example, sharks and rays would be distinctly separated from bony fish on a wide range of characters (e.g. scale form, collapsibility of fins, mouth position, opercle characters), despite having some similar functional specialisations. In other words, we anticipated that the functional specialisations of a demersal feeding shark would be more closely related to those of other demersal feeders, than to those of a pelagic shark. Thus we developed a method to emphasise the functional and de-emphasise the phylogenetic relationships.

Our method involved three steps as follows:

1. **Morphotypes** (groupings of species with similar morphology) are expected to be identified by including all characters in an unguided analysis. Due to our 'shotgun' selection of both traditional and functional characters, we expected that this analysis would identify family groups and, on basis of the traditional characters, form clusters of closely related species.

2. **Ecomorphotypes** (groupings of species reflecting ecological function) were expected to be identified by analysing the data using subsets of characters related to three key ecological functional areas (feeding, self-preservation and productivity— see next section). Each ecomorphotype was defined by a distinct profile of group association over the three key functional areas. By specifically targeting characters related to a particular ecological function we expected these, and not phylogeny, to drive the multivariate groupings. To test our assumption that these groupings were driven primarily by ecological function we used PCC to compare ecomorphotypes with ecological/ environmental factors.

3. **Rapid assessment** - the identification of ecomorphotypes by rapid assessment was tested by reanalysing the data using only characters contributing strongly to between-group differences in the GSTA for each of the ecomorphotype analyses, or contributing strongly to the final ecomorphotype groups based on all characters. The technique was considered successful if it reproduced the ecomorphotype groupings observed in Step 2, and from a substantially reduced character-set.

4.4.1 Ecosystem functional areas

Evolutionary fitness of organisms can be measured by their ability to survive and produce offspring (*sensu* Alexander 1967). For this an organism has to feed effectively and be able to avoid and/or deter potential predators; furthermore, it has to have a reproductive strategy that maximises potential contribution to the next generation while minimizing compromises on the survival strategy. Based on this general statement, we focussed our analysis on three ecosystem functional areas: feeding, self-preservation/predator avoidance and productivity. Locomotion is highly important in several aspects of feeding and predator avoidance; therefore, it was treated as a separate functional area. Each of these functional areas was subdivided on a functional basis for character identification (see below). However, no subdivisions were retained in the analysis. The functional areas and their subdivisions were:

Locomotion: acceleration speed; top speed; endurance; manoeuverability (in the watercolumn and on the substrate); buoyancy control

Feeding: foraging method (including locomotion); prey detection; prey capture; prey handling; digestion

Self-Preservation/ Predator avoidance (size/camouflage/hiding): predator detection; predator evasion (including locomotion and camouflage/hiding); mechanical defence (armouring); chemical defence

Productivity: growth rate; fecundity; breeding strategy (life bearer/migration to special breeding grounds)

Morphological characters that influence the animal's performance in the defined functional areas were identified from the literature (Table 4.4.1.1); Appendix 5 contains a detailed list of the characters used in each of the ecomorphotype analyses. Unfortunately, we could not collect any relevant morphological data for the productivity functional area – the occurrence of ripe specimens for the collection of egg size, gonad weight, etc. was rare, due to the opportunistic sampling regime. Hence, the possible implications of different life history strategies and productivity will only be considered in the discussion, referring to maximum size, age and mortality data summarised in Table 4.2.3.1 and detailed the SEFEHS report (Bax and Williams, 1999).

Table 4.4.1.1 Ecosystem functional areas and their relevant characters derived from the literature

Type/mode	Characters involved (italics: characters not recorded in this project; bold: general functions)	References
LOCOMOTION (L)		
Acceleration speed (L1)	Dorsal/anal fins: position size (area/base)	Videler (1993); Helfman (1997)
	Caudal fin: aspect ratio (CAR = (height)2 / area), shape, rigidity, scales	Helfman (1997); Webb (1984)
	Peduncle depth	Helfman (1997): Webb (1984)

Type/mode	Characters involved (italics: characters not recorded in this project; bold: general functions)	References
	Body shape (ratios depth/width/length): reasonably streamlined, elongate, deep tail	Webb (1984); Videler (1993)
	Body rigidity (scale size, type and overlap)	Videler (1993); Helfman (1997)
	Muscle content (abdominal muscle thickness, fillet width/depth)	Webb (1984); Videler (1993)
Top speed (L2)	Muscle content (abdominal muscle thickness, fillet width/depth)	
	Overall size: body length	Whitehead (1975)
Endurance (at speed) (L3)	Peduncle depth/width	Videler (1993); Webb (1984); Helfman (1997)
	Keel / Finlet	Videler (1993); Helfman (1997)
	Caudal fin: CAR, shape, rigidity, scales	Videler (1993); Webb (1984); Helfman (1997); Gosline (1971); Whitehead (1975)
	Body shape (ratios depth/width/length, include body wgt.): fusiform	Webb (1984); Videler (1993)
	Body rigidity (scale size, type and overlap)	Webb (1984); Helfman (1997); Whitehead (1975)
	Fins collapsibility, position, (sheeth on pelvic)	Whitehead (1975); Alexander (1967)
	Muscle content (abdominal muscle thickness); red muscle	Helfman (1997)
	Gill filament area (include aspect ratio and flexibility)	Alexander (1967)
	Pectoral fins: rigidity, scales	Helfman (1997)
	Eye: mobility, position (fast swimmers: covered with adipose tissue)	Jobling (1995)
Manoeuvrability (in the watercolumn) (L4)	Pectoral fins: shape, angle, rigidity, pectoral fin aspect ratio (PAR = max height/max depth), base, position	Harder (1975); Webb (1984); Helfman (1997); Gosline (1971)
	Pelvic fins: shape, position, area, rigidity, scales, (base)	Harder (1975); Webb (1984); Helfman (1997); Gosline (1971)
	Body shape (ratios depth/width/length, include body wgt): diamond	Videler (1993); Webb (1984); Helfman (1997); Alexander (1967)
	Caudal fin: shape, CAR	Whitehead (1975); Gosline (1971)
	Dorsal/anal fins: hight, area, rigidity, scales	Gosline (1971); Videler (1993); Helfman (1997); Alexander (1967); Nikolski (1963)

Type/mode	Characters involved (italics: characters not recorded in this project; bold: general functions)	References
	Buoyancy (swim bladder/liver)	Videler (1993); Alexander (1967)
Manoeuvrability (on substrate) (L5)	Fins: 'locomotory' = walking	Nikolski (1963); Helfman (1997)
	Body shape (ratios depth/width/length, include body wgt): flattened or burrowing/eel shape	Nikolski (1963); Harder (1975); Videler (1993)
	Pectoral fins: shape, angle, rigidity, base, position (standing start)	Gosline (1971); Helfman (1997)
Buoyancy control (L6)	Swim bladder	Alexander (1967); Whitehead (1975)
	Liver: weight, size	Alexander (1967); Whitehead (1975)
	Paired fins: position, angle, shape	Alexander (1967); Videler (1993)
	Lipid and/or water content of flesh	Alexander (1967)
FEEDING (F)		
Foraging method (passive/ambush/stalk/ lunge/chase/probe) (F1)	Locomotion (manoeuvrability, acceleration, high speed)	Helfman (1997);Norton (1995)
	Camouflage	Videler (1993)
	Mouth position, size, angle	Helfman (1997); Alexander (1967)
	Maxilla extension (round vs. grinning mouth)	Gosline (1975); Alexander (1967)
	Tubular snout	Gerking (1994); Jobling (1995)
	Fin modifications: lures	Gerking (1994); Whitehead (1975)
Prey detection (F2)	Eye: size, position, mobility	Gosline (1971); Jobling (1995)
	Sensory pores	Alexander (1967); Gosline (1971); Jobling (1995)
	Lateral line system	Alexander (1967); Gosline (1971); Jobling (1995)
	Gustatory appendages: barbels, oral papillae	Gosline (1971); Helfman (1997); Whitehead (1975); Jobling (1995)
	Smell: nostrils development/nasal tentacles	Gosline (1971); Jobling (1995)
	Fins: tactile	Helfman (1997); Whitehead (1975)
	Electric organs	Jobling (1995); Whitehead (1975)

Type/mode	Characters involved (italics: characters not recorded in this project; bold: general functions)	References
Prey capture process (biting/filtering/ram/ suction) (F3)	Mouth dentition: type, size, number rows (include tongue development)	Helfman (1997); Gosline (1975); Alexander (1967); Gerking (1994); Norton (1995); Wootton (1992); Whitehead (1975); Jobling (1995)
	Gill rakers: length, spineation, spacing, flexibility, (include area/aspect ratio)	Helfman (1997); Gerking (1994); Alexander(1967); Wootton (1992); Whitehead (1975); Jobling (1995)
	Premaxillary protrusion	Helfman (1997); Gosline (1975); Alexander (1967); Kotrschal (1989)
	Maxilla extension (round vs. grinning mouth)	Gosline (1975); Alexander (1967)
	Head size: depth, width, length	Alexander (1967)
	Opercular opening (for pump action)	Gerking (1994); Jobling (1995)
	Gape size	Gerking (1994); Alexander (1967); Whitehead (1975)
	Lips	Alexander (1967)
Prey handling (whole/biting/grinding/ crushing) (F4)	Gape: height, width, area, tooth depressability	Helfman (1997); Gerking (1994); Norton (1995)
	Pharyngeal gape	Helfman (1997)
	Dentition: type, size, number rows (include tongue development)	Helfman (1997); Alexander (1967); Gosline (1971)
	Jaw strength / musculature	Norton (1995); Gosline (1971)
Digestion (F5)	Gut length	Adite and Winemiller (1997); Wootton (1992); Jobling (1995)
	Foregut length (oesophagus to pylorus)	Jobling (1995)
	Stomach: presence, length, muscularity, acidity	Wootton (1992); Whitehead (1975); Jobling (1995)
	Pylorus: caeca count, length	Wootton (1992); Jobling (1995)
	Body cavity colour	Whitehead (1975)
SELF-PRESERVATION (CP)		
Camouflage/hiding (size, camouflage/hiding) (C)	Colouration	LeDanois (1957); Nikolski (1963);

Type/mode	Characters involved (italics: characters not recorded in this project; bold: general functions)	References
camouflage/hiding) (C)		Nikolski (1963); Jobling (1995); Whitehead (1975)
	Pattern	LeDanois (1957); Nikolski (1963); Jobling (1995); Whitehead (1975)
	Countershading	LeDanois (1957); Whitehead (1975)
	Modified appendages	Whitehead (1975)
	Eye stand-up	Nikolski (1963)
	Pelvic body width (sharply keeled: less visible from below)	Whitehead (1975)
	Body shape/size (depth, width, length)	Whitehead (1975)
	Shoaling	Whitehead (1975)
Predator detection (P2)	Eye: size, mobility, position	Jobling (1995)
	Motion sensors: lateral line, sensory pores	Jobling (1995); Alexander (1967)
	Smell: nostril development/nasal tentacles	Jobling (1995); Gosline (1971)
	Alarm reaction: release of alarm substance by attacked fish	Jobling (1995)
Predator avoidance (speed/manoeuverability/ size) (P3)	Locomotion (high speed, acceleration, manoeuvrability)	Whitehead (1975)
	Camouflage/hiding	Whitehead (1975)
	Body shape/size (depth, width, length)	Whitehead (1975)
Mechanical Defence/Armouring (spines/scales) (P4)	Dorsal fin shape, height, modification, ability to interlock	Jobling (1995); Whitehead (1975)
	Presence of spines: on fins, opercula, head, tail, body	Jobling (1995); Whitehead (1975)
	Scale modifications	Jobling (1995); Whitehead (1975)
	Enlarging the size by inflating body	Whitehead (1975)
Chemical defence (poison/taste bad) (P5)	Poison glands	Jobling (1995); Whitehead (1975)
	Accumulation of poisons of food in flesh	Jobling (1995); Whitehead (1975)
	Conspicuous, 'bad taste' colouration (mimicking/real)	Whitehead (1975)
	Electric organ	Whitehead (1975)

4.4.2 Character set reduction for a rapid assessment approach

In order to achieve a rapid assessment technique we needed to reduce the character-set, while retaining the ecomorphotypes we had identified. Clarke and Warwick (1998) proposed a stepwise process for extracting a series of data-subsets, that have multivariate response patterns which closely match that of the complete data set. This method presents an objective way of reducing the data-set by ensuring that the SSH and cluster analysis patterns are not greatly changed. However, considering the vast size of our data matrix it was logistically not feasible to use this method. Furthermore, Clarke and Warwick's (1998) method is based on calculating a Spearman correlation between the entries in the similarity matrix of the respective subsets and the similarity matrix of the complete data-set, a matrix which did not have for ecomorphotypes, as they were identified based on three separate analyses.

Therefore, instead of this stepwise approach, we based the character subsets to be tested on the Kruskal-Wallis and χ^2 values from GSTA analyses. The χ^2 values were calculated separately for each of the three functional areas – locomotion, feeding and self-preservation – or for the ecomorphotypes, as defined by the combination of the functional areas. Reduced character subsets were created using either characters with Kruskal-Wallis or χ^2 values >80 and >70, or the 30 highest ranking characters in the GSTA. In the second approach, the 10 highest ranking characters were chosen from each analysis, characters that featured importantly in more than one functional area were given a weighting of 1 for each functional area in which they were important in discriminating groups. Further character reduction was tested by increasing weighting on the highest ranked characters of a highly correlated set of interval and/or ratio type characters (Pearson's correlation r^2>07), or reducing weighting on the lower ranked ones.

Cluster analyses were performed on the reduced character-sets and the resultant groupings compared to the ecomorphotypes from the full functional area character-sets to test the respective character sets.

5 RESULTS / DISCUSSION

5.1 Performance of a new approach to the analysis of ecomorphology data

Extensive comparison of the properties of available similarity measures and multivariate statistical methods resulted in the development of a new approach to the analysis of ecomorphology data (Section 4.3.2). In the course of our research we tested Gower's weighting of hierarchical characters (Formula (2)). For this we examined a set of archetypal fish, F1-F6 (Figure 5.1.1), that differ in selected characters (Table 5.1.1) and calculated a Gower similarity Matrix (Table 5.1.2) for this data set.

Table 5.1.1 Test dataset of archetypal fishes F1-F6 for the examination of the performance of hierarchical character similarity measures (for a diagrammatic representation of F1-F6 see Figure 5.1.1)

Fish	Eye position	Pectoral fin present	Pectoral fin rays	Pectoral fin shape	2nd dorsal fin present
Data type	Non-hierarchical	Hierarchical primary	Hierarchical secondary	Hierarchical secondary	Non-hierarchical
Range	2	1	2	2	1
F1	1	1	1	1	1
F2	1	1	1	2	1
F3	1	1	2	2	1
F4	2	1	1	1	1
F5	1	0	-	-	1
F6	2	0	-	-	1

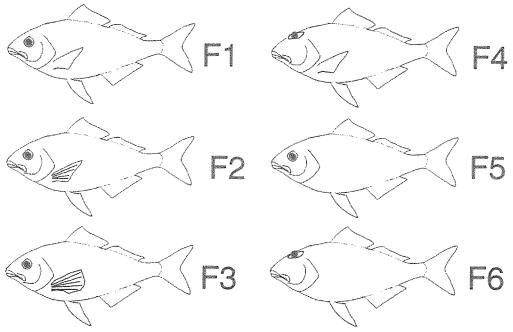


Figure 5.1.1 Diagrammatic representation of 6 archetypal fish differing in specifically chosen characters, for the purpose of testing the hierarchical similarity indices

Table 5.1.2 Similarity Matrix for F1-F6, obtained by applying Gower's (1971) hierarchical similarity measure (Formula (2)) to the data in Table 5.1.1

Similarity	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**
F1	1					
F2	1	1				
F3	1	1	1			
F4	0.900	0.889	0.875	1		
F5	0.500	0.571	0.667	0.375	1	
F6	0.375	0.429	0.500	0.500	0.900	1

Gower's (1971) way of dealing with hierarchical characters proved inappropriate in our situation. It does not distinguish between fish (samples) that differ only in secondary characters – F1 has a similarity of 1 with itself (S(F1,F1)), as well as with F2 (S(F1,F2)) and F3 S(F1,F3)), although F2 has fin rays and F3 has fin rays and a different fin shape. However, this subtle difference can be observed, when comparing a fish (sample) that not only differs in secondary hierarchical characters, but also in primary and/or non-hierarchical characters: S(F1,F4) > S(F2F4) > S(F3,F4). Furthermore, this trend is reversed if the primary hierarchical character is absent: S(F1,F5) < S(F2,F5) < S(F3,F5). The latter is caused by our definition of absent values. Due to the nature of our data we valued the occurrence of an absence as importantly as the occurrence of a presence.

In comparison to Gower's hierarchical similarity, the new measure developed for the present study performed, overall, according to our expectations (Table 5.1.3).

Table 5.1.3 Similarity Matrix for F1-F6, obtained by applying our new, hierarchical similarity measure with w_p=0.1 (Formula (3)) to the data in Table 5.1.1

Similarity (w_p=0.1)	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**
F1	1					
F2	0.878	1				
F3	0.756	0.878	1			
F4	0.878	0.756	0.634	1		
F5	0.488	0.488	0.488	0.366	0.512	
F6	0.366	0.366	0.366	0.488	0.390	0.512

This form of weighting reflects the increasing difference in secondary characters in decreasing similarity values, regardless of any other characters – S(F1,F1) > S(F1,F2) > S(F1,F3) and S(F4,F1) > S(F4,F2) > S(F4,F3). It also weighs a secondary hierarchical character at the same level as a non-hierarchical character – S(F1,F2) = S(F1,F4) = S(F2,F3). This latter characteristic results in rather low similarity values when fish (samples) with a high degree of absent hierarchical characters are compared – including comparing such fish (samples) with themselves (cf. S(F1,F5) = 0.488, S(F5,F5) = 0.512).

The occurrence of a self-similarity smaller than 1 is related to the object under observation not meeting the requirements that the observer expects, by missing one or more primary characters. Thus, such an object cannot achieve the same level of self-similarity as one that exhibits the complete character set. To achieve similarity values that allow direct comparison across all species we chose not to alter our effective character-set used for comparison, according to what characters were present, but rather accepted self-similarity values smaller than one. The self-similarity of fishes F5 and F6 in the test data-set are extremely low, since the data was chosen to highlight the effect of hierarchical character presence/absence. In the real data of the present study the effect of absence in hierarchical characters is moderated by non-hierarchical characters. Figure 5.1.2 shows the distribution of the between species similarity compared to the self-similarity values for each species for each of the analyses discussed in the following section. Furthermore, a test of the effect of this reduced self-similarity was conducted by repeating the morphotype analysis – i.e. calculating a similarity matrix followed by a cluster analysis based on the complete character-set – with each species representative doubled. The 16 groups defined in the morphotype analysis could be identified again (only *E. nitidus nitidus* changed group membership) and as we expected, each species grouped the closest to itself in the cluster analysis.

The weighting factor (w_p) in Formula (3) is left to the discretion of the observer. We tested the initial value of 0.2 as well as 0.1 and 0.3, the resulting similarity matrices of which are in Tables 5.1.4, 5.1.3 and 5.1.5, respectively. Increasing w_p results in an increase/decrease in the similarities, where a match/mismatch in the primary characters is recorded. It can therefore be

used to increase the significance of the primary character over the importance of the secondary characters. In the present study we decided on the use of $w_p = 0.1$, as more interest lies in the detail of the secondary characters (e.g. fin structures, or teeth types).

Table 5.1.4 Similarity Matrix for F1-F6, obtained by applying our new, hierarchical similarity measure with w_p=0.2 (Formula (3)) to the data in Table 5.1.1

Similarity (w_p=0.2)	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**
F1	1					
F2	0.881	1				
F3	0.762	0.881	1			
F4	0.881	0.762	0.643	1		
F5	0.476	0.476	0.476	0.357	0.524	
F6	0.357	0.357	0.357	0.476	0.405	0.524

Table 5.1.5 Similarity Matrix for F1-F6, obtained by applying our new, hierarchical similarity measure with w_p=0.3 (Formula (3)) to the data in Table 5.1.1

Similarity (w_p=0.3)	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**
F1	1					
F2	0.884	1				
F3	0.767	0.884	1			
F4	0.884	0.767	0.651	1		
F5	0.465	0.465	0.465	0.349	0.535	
F6	0.349	0.349	0.349	0.465	0.419	0.535

We succeeded in our quest for a similarity measure that accommodates mixed attribute data as well as hierarchically dependent variable sets by using a combined, hierarchically weighted similarity index (Formula (3)).

In Belbin's combined use of separate similarity measures we found a statistically sound method of calculating a similarity matrix from mixed attribute data. Furthermore, As shown here, our way of dealing with the hierarchical data also proved successful, although this method resulted

in self-similarity values smaller than 1 for species with missing primary characters. This situation was sub-optimal but it proved to be the best solution to the problem of comparing a large variety of highly diverse organisms, and in practice there was little overlap of between species similarities and self-similarities (Figure 5.1.2). With the weighting of the primary and secondary hierarchical characters we decided to emphasise the latter, since for most structures of fish morphology presence or absence is important, however their functionality is in their detailed construction and positioning.

Discussion

As noted (Sections 1.4 and 4.3.2), mixed attribute data and hierarchical variables have been analysed in many recent ecomorphology studies, using standard, though unsuitable statistical techniques such as PCA and CCA (e.g. Watson and Balon 1984; Wikramanayake 1990; Norton 1995; and Motta *et al.* 1995a). Discussion with Kathy Haskard – CSIRO statistician – and Leigh Belbin made us aware of the shortfall of these studies to account for the intrinsic problems of ecomorphology data analysis. In an attempt to solve these we considered a variety of specialised analysis techniques, in particular the Gower hierarchical similarity index (Gower 1971) and Belbin's combined use of separate similarity measures (Belbin pers. comment). Unsatisfied with the performance of either method, we combined and adapted them to develop a new similarity index and weighting system that accommodates mixed attribute data and hierarchical variables. Based on the similarity matrix obtained using this index we could use any non-linear ordination technique.

We did not attempt to account for the inherent non-independence of species as samples in statistical analyses due to their evolutionary background (*sensu* Felsenstein 1985). The cladistic relationships of the families and species covered in the present study are not well enough understood to allow for an accurate statistical correction as proposed by Felsenstein (1985). Hence, we preferred to knowingly ignore the problem rather than solving it based on wrong assumptions. Future ecomorphological analyses will have improved power to isolate ecomorphotypes if they can account for phylogenetic similarities in their analysis.

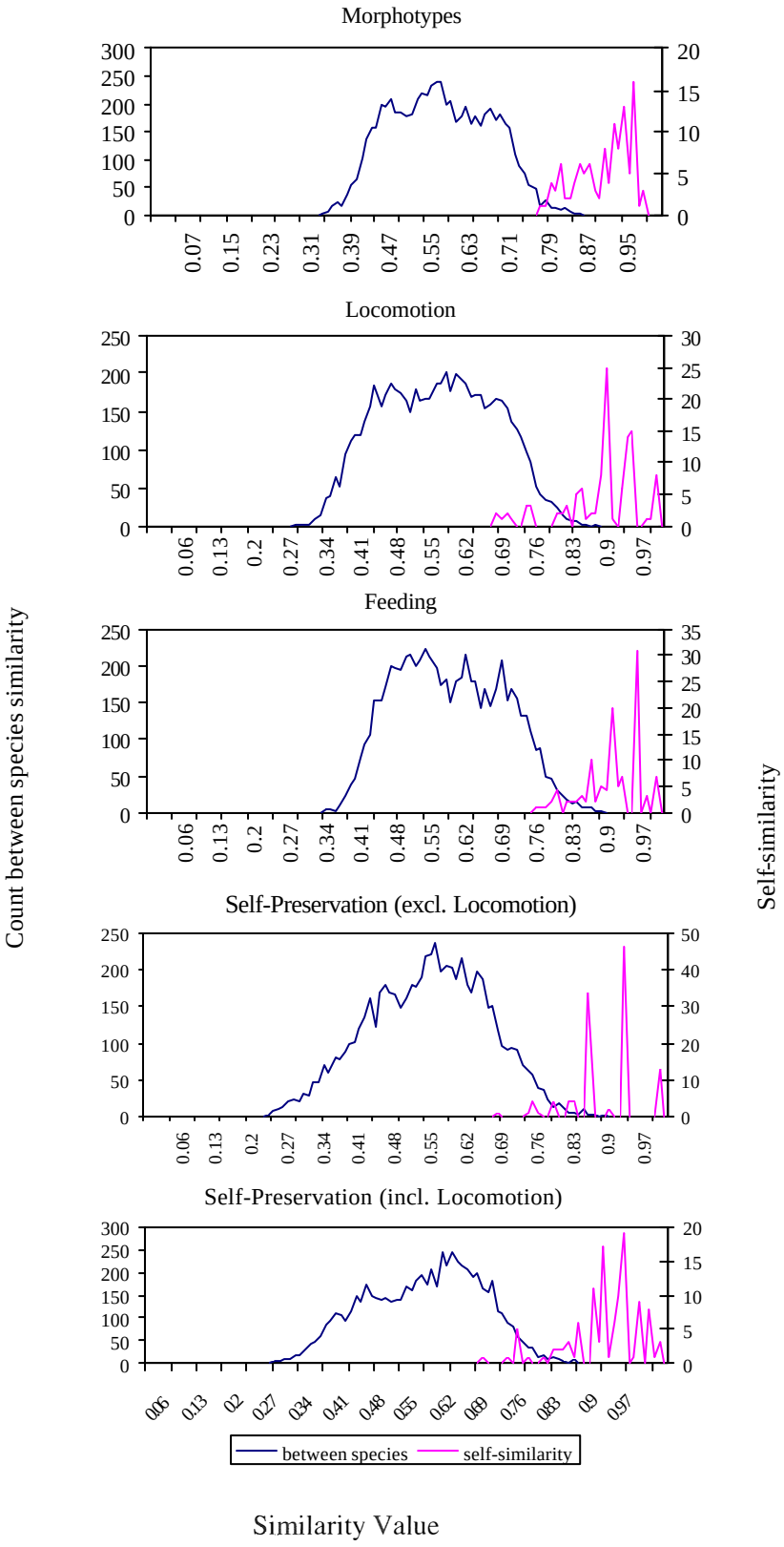


Figure 5.1.2 Frequency distribution of between species similarity and self-similarity values for each of the analyses described in section 5.2

5.2 Data analysis

5.2.1 Morphotypes

Cluster analysis of all characters (Appendix 5) for all fishes (1 fish per species) resulted in a strongly phylogenetic grouping of the species, i.e. grouping was primarily by family or by higher taxa (Figure 5.2.1.1). At a dissimilarity of 0.629 six broad, distinct groups are identified: two groups of Elasmobranchii: true sharks, (I), and rays (II); and four groups of Teleostei: two mixed groups (III, including *C. milii* – a member of the Holocephali, and V), *G. parsinus* (IV), and pleuronectiformes (VI). A lower level split (0.443 dissimilarity) results in 16 groups where co-familials and groups of closely related families can be identified more clearly. All true shark families still group together (group1); the rays (group 2) also stay in one group, with exception of *H. monopterygium,* which forms its own group (3). Similarly, *C.milii* separates out to form its own group (8). *G. parsinus* (group 4) still stands on its own. The pleuronectiform families Bothidae and Pleuronectidae together form group 5, while the Diodontidae and Tetraodontidae form group 14. Single family groups are: Zeidae (9), Macroramphosidae (16), Monacanthidae (13) and Aracanidae (15). The last three groups (6, 7 and 12) are composed of a series of families.

These groups also separate clearly in a 3-d SSH plot (stress=0.15) indicating the robustness of the cluster analysis (Figure 5.2.1.2). Because ordination plots such as those resulting from SSH analysis do not directly relate original characters to the plot axes (Section 4.3.3), PCC analysis was used to identify the characters driving the direction of group-splits. The most obvious directions in the orientation of the figure were associated with highly correlated characters (PCC correlation $|r|$ >0.7). These include front left to back right (body and head width), centre back to front (decreasing lateral line development and mouth teeth types), and bottom left to the top right (increasingly central positioning of the pectoral fin and specialisation of the scales, increasing body and head depth, decreasing pharynx to pylorus length, and the presence of a swim bladder) (Figure 5.2.1.3). The species composition of groups and an overview of species' body shapes are shown in Plate 1.

Discussion

As we expected, the unguided analysis using all characters resulted in a grouping that strongly reflects phylogenetic relationships. Our complete character-set contains many of the standard taxonomic characters used by taxonomist to differentiate species and higher taxa. In particular, the important characters driving our morphotype analysis – relative body proportions (body and head compression indices), fin structure and positioning, scale morphology and lateral line – are all fundamental characters for taxonomy of temperate Australian fishes (e.g. Gomon *et al.* 1994).

Underlying the phylogenetic split, however, a clear functional pattern is also apparent. Decreased dorso-ventral flattening of the body and increased fin specialisation from bottom left to top right of the SSH plot results in a segregation of fishes of sediment flat habitats (e.g. rays, group 2), from pelagic fishes (e.g. Carangidae and Centrolophidae, group 7), and, in turn, from fishes more typically associated with structured habitat (e.g. Labridae, Cheilodactylidae and

Pentacerotidae, group 12). This exemplifies the basic link between taxonomy and ecological functionality (*sensu* Douglas and Mathews 1992).

Satisfied that the analysis of all species using all characters, the 'shotgun approach', resulted in the identification of morphotypes, strongly guided by phylogenetic affinity, we embarked on the second step of the analytical strategy. Here characters were selected according to their specialisation for specific ecological functions with the aim of identifying ecomorphotypes.

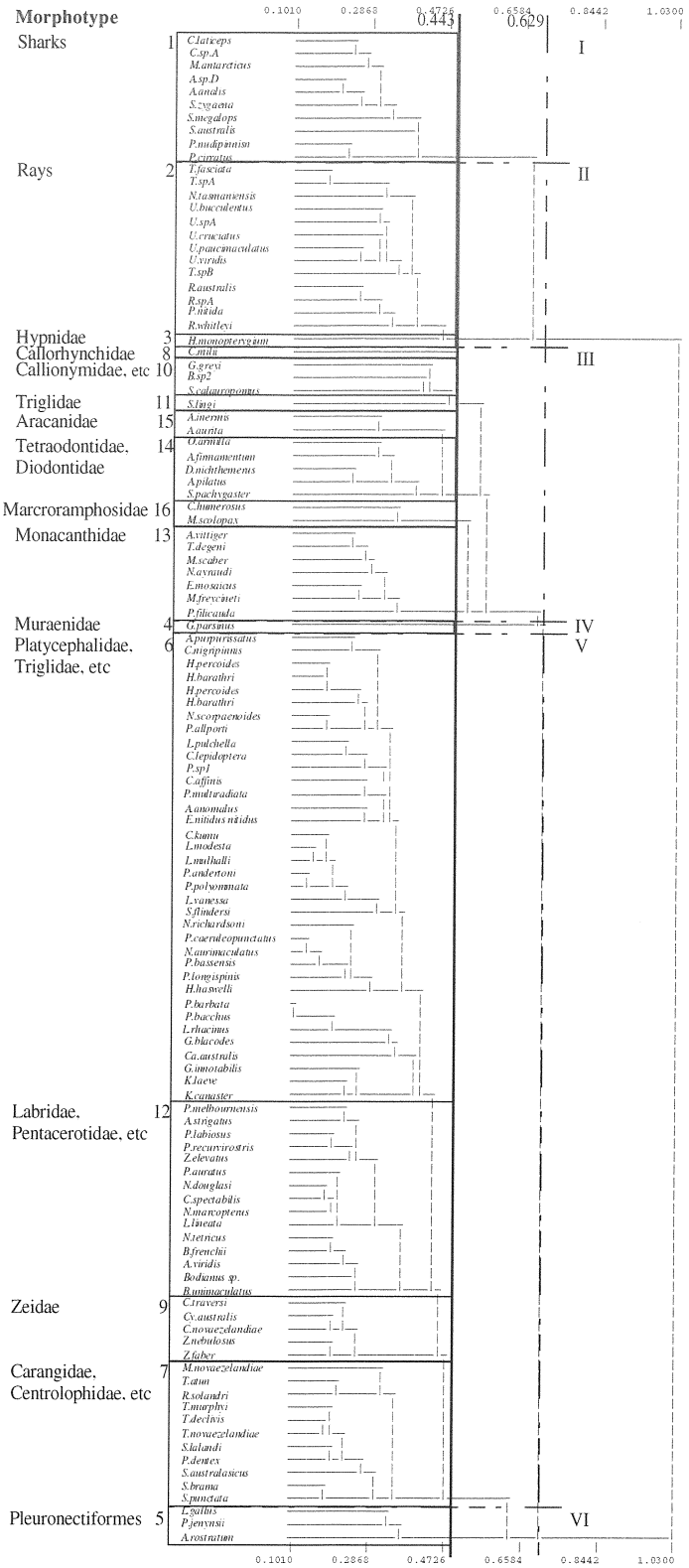


Figure 5.2.1.1 Agglomerative cluster analysis of the dissimilarity matrix of 114 species, based on all characters measured (63 measurements, 139 coded characters). Groups indicated: I-VI split-off level =0.629 dissimilarity; 1-16 split-off level =0.443 dissimilarity

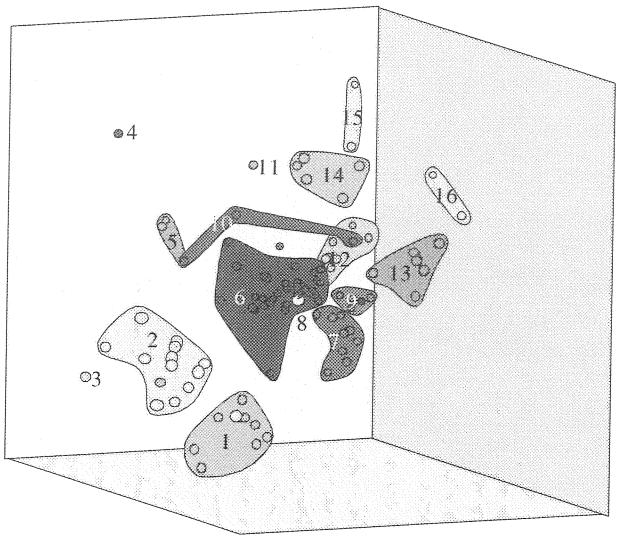


Figure 5.2.1.2 Morphotypes: SSH of the dissimilarity matrix of 114 species, based on all characters measured (63 measurements, 139 coded characters); stress =0.15. Groups were identified in the hierarchical cluster analysis.

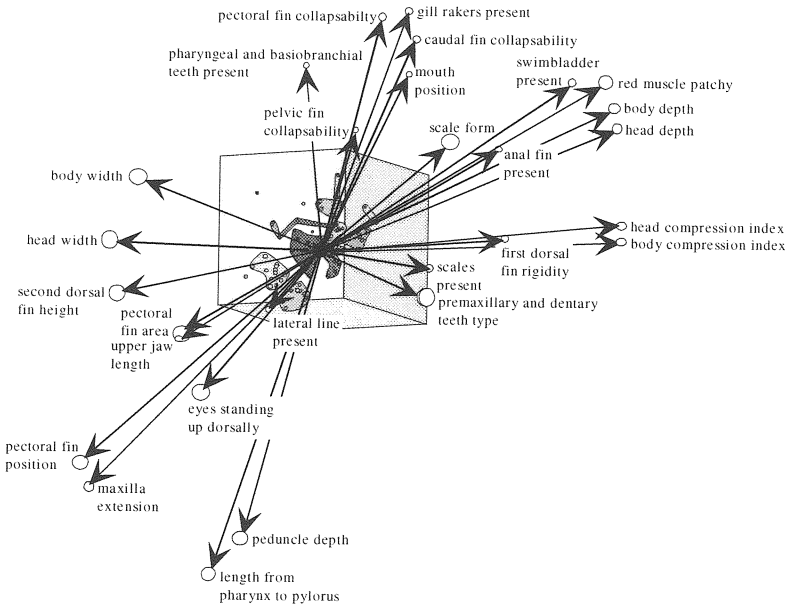


Figure 5.2.1.3 Intrinsic data PCC of the Morphotype SSH showing the direction of the best linear fit of characters with $|r| > 0.7$ in the ordination space, using unit vectors (circle size indicates the third dimension: large in the front, small in the back)

5.2.2 Ecomorphotypes

Locomotion

Cluster analysis of all species (one fish each) using only characters related to locomotion - 36 measurements and 52 coded characters (16 non-hierarchical, 10 primary and 62 secondary hierarchical characters; Appendix 5) - resulted in a primary split at 1.050 dissimilarity, separating sharks, rays and pleuronectiformes from the rest (Figure 5.2.2.1). On a lower level (0.512 dissimilarity), there was a 9 group split. The groups formed are true sharks, including *Callorhinchus milii* (9), rays (1), *Hypnos monopterygium* (2), Pleuronectiformes (3), *Gymnothorax parsinus* (6), Aracanidae, Tetraodontidae and Diodontidae (5), and three teleost groups divided into fishes with narrow necking and strongly forked caudal fins (Carangidae, Centrolophidae, Gempylidae and Scombridae; 8); elongate, round to dorso-ventrally flattened fish with deep peduncle (e.g. Platycephalidae, Moridae, Triglidae; 4), and group 7 with discoid and more laterally compressed species (e.g. Zeidae, Monacanthidae, Pentacerotidae, but also Labridae and Cheilodactylidae).

The grouping in the relatively low-stress (0.15) 3-d SSH (Figure 5.2.2.2) is consistent with the cluster analysis. The species composition and body shapes of groups are shown in Plate 2. Interpretation by PCC (Figure 5.2.2.3) identified a gradient from the bottom front to top back (increasing body and fillet depth and decreasing body width), and a left to right trend (decreasing area and increasingly central position of the pectoral fin). The bottom front to top back trend was used to number the groups sequentially according to their separation in the SSH-plot.

GST analysis of each group compared individually to all other fish resulted in a ranking of characters, according to their discriminatory power for the respective locomotory group. The rays (group 1 – e.g. Urolophidae, Rajidae) are defined primarily by the non-collapsibility of their fins, the specialised central positioning of the pectorals, their low peduncle depth and BCI as well as their pectoral fin area. Group 2 (*H. monopterygium*) separates due to its long-based pelvic fins and by the low pectoral fin aspect ratio. This measure is peculiar in this species, when compared to other rays, as the pectoral fins only take up a small area of the body width with the bulk being formed by electric tissue. Pleuronectiformes (group 3 – Bothidae and Pleuronectidae) are distinguished, within our functional definition of their body-plan, by the absence of pelvic and anal fins, and the long-based, forward set pectoral fins. In group 4 fishes (e.g. Platycephalidae, Moridae, Triglidae) anal and second dorsal fin areas and bases are particularly large. Furthermore, the pectoral fin base is long, the gill filaments are short, the peduncle rather wide and the abdominal musculature well developed. Group 5 (Aracanidae, Tetraodontidae and Diodontidae), on the other hand, is distinguished by the absence of pelvic fins, a back-set anal fin, and a large swimbladder volume. Group 6 (*G. parsinus*) is defined mainly by the lack of lateral appendages, but also by a rounded, highly elongate body shape. Group 7 fishes (e.g. Zeidae, Monacanthidae, Labridae) have a high BCI, which translates into a discoid body shape, back-set and high first dorsal fins, relatively large swimbladders, and collapsible caudal and pectoral fins. Fishes of group 8 (Carangidae, Centrolophidae, Gempylidae and Scombridae) are marked by the frequent presence of finlets and strongly developed keels, along with the rather rigid, long gill filaments and the ability to collapse the pelvic fin completely into a grove, but also by the back-set first dorsal and the previously mentioned deeply forked shape of the caudal fin. Finally the true sharks and *C. milii* (group 9 –

e.g. Scyliorhinidae, Squalidae, Pristiophoridae) separated out due to the presence of scales on, and the non-collapsibility of all their fins, but also due to their rather high PCI, and large size.

Discussion

The groupings defined by the cluster analysis of locomotory characters clearly reflected four basic swimming modes: undulatory, oscillatory, anguilliform and sustained swimming (Videler 1993; Helfman *et al.* 1997). We used these as a basis for naming the locomotion ecomorphotypes identified here.

The first three groups are formed by fishes that employ an undulatory swimming style. The rays (group 1 – 'undulatory swimmers') use their pectorals in an undulatory fashion (Videler 1993; Helfman *et al.* 1997); *H. monopterygium* (group 2 – 'undulatory slow swimmer') moves similarly, but the reduced aspect ratio of its pectoral fins, due to the electric tissue, results in reduced mobility of this species. The pleuronectiformes (group 3 – 'undulatory/burst swimmers') also employ a similar swimming mode, using their dorsal and anal fins, which we defined as 'functional pectorals', but also have a well-developed tail for burst swimming.

Sustained swimmers or 'cruisers' fall into two groups. Group 8, 'cruiser (caudal)', have a deeply forked/lunate caudal fin and narrowly necked peduncle (Moyle and Cech 1988; Videler 1993; Helfman *et al.* 1997). Sharks (group 9 – 'cruiser (anguilliform)') are also sustained swimmers, but they have a fundamentally different swimming style to teleost fish. Sharks use anguilliform movement, even for sustained swimming, and have a body plan with dorsal and anal fins positioned to maximise efficiency in this form of locomotion (Webb 1984; Helfman *et al.* 1997).

Oscillatory swimming modes are employed by two groups, both of which have well developed swimbladders allowing for precise buoyancy control and therefore precise manoeuvring. The groups differ in the fins principally involved in propulsion: Aracanidae, Diodontidae and Tetraodontidae (group 5 – 'oscillatory manoeuvrer (caudal)') use the caudal fin, while group 7 ('oscillatory manoeuvrer (pectoral)') mainly use their pectoral fins (Webb 1984; Weihs 1989; Helfman *et al.* 1997). Monacanthidae and Zeidae form a subgroup in group 7, they also employ undulatory movement of the anal and dorsal fins for slow manoeuvres (Lighthill and Blake 1990).

Only one 'burst swimmer' group (group 4) of fish with elongate bodies, deep tails and long-based anal and second dorsal fins (Webb 1984; Moyle and Cech 1988), was identified. A rather odd member of this group was *Brachionichthys sp.2*, the Australian handfish. Although this species does have a relatively deep, muscular tail that is increased in size by a high second dorsal and anal fin, the presence of locomotory pectorals suggest another mode of locomotion. *In situ* observations of handfishes have shown that they mostly use their hand-like pectorals to walk on the substrate, but that they use their tail for burst of swimming when they are disturbed (Green, CSIRO pers. comment). Hence, while the body seems to be shaped for burst swimming, this is only used as an escape response. Apparently, the single, secondary character 'locomotory pectoral fins' was not strong enough to separate this species from the other burst swimmers.

'Anguilliform swimmer' (group 6) use snake or eel-like movements of a highly elongate, thin body for propulsion. *G. parsinus*, is the only member of this group, also being the only eel in the present study.

Within two of the basic swimming modes, undulatory and sustained swimming, elasmobranchs and teleosts form parallel groups. It could be argued that we did not entirely succeed in separating functional from taxonomic characters in these cases. However, most characters functional in locomotion (e.g. body and peduncle shape, fin structure, or the presence of fin-scales) also have distinct taxonomic value for the distinction between elasmobranchs and teleosts. Furthermore, although the resultant swimming mode corresponds between Pleuronectiformes and rays, and sharks and the 'sustained swimmer (caudal)' group, respectively, the way it is achieved differs between the groups.

The characters that determine the broad-scale groupings tend to mask subtle differences between co-familials. For example, within the 'burst swimmers' fish with and without swimbladder are grouped together; however, it may be expected at a finer level analysis, that these types group apart – in fact, an indication of such a separation is present in the cluster analysis (Figure 5.2.2.1). This would result in an interesting separation of *Neoplatycephalus richardsoni*, the only member of the Platycephalidae with a functional swimbladder in this study, from its co-familials. In the present study we have limited our scope to determining broad-scale ecomorphotypes only, due to the number of families included.

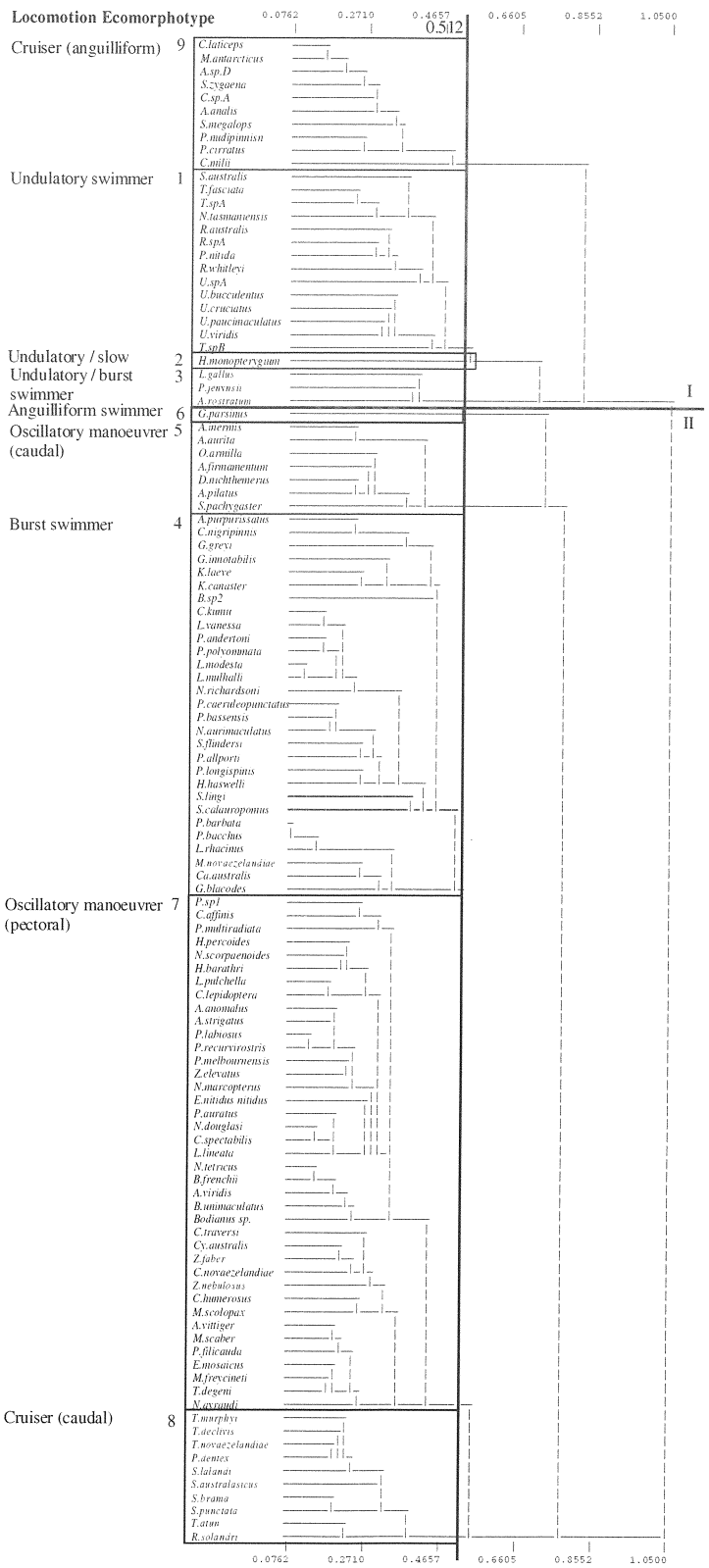


Figure 5.2.2.1 Agglomerative cluster analysis of the dissimilarity matrix of 114 species, based on characters related to locomotion (36 measurements, 62 coded characters). Groups indicated: 1-9 split-off level =0.512 dissimilarity

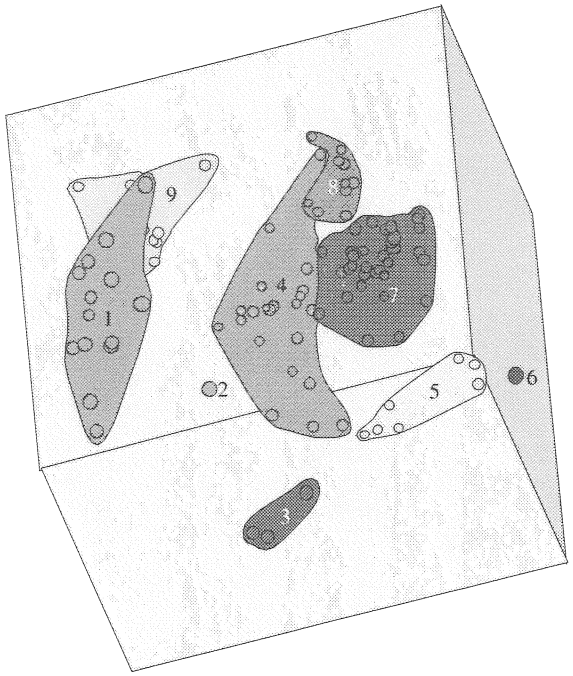


Figure 5.2.2.2 Locomotion Ecomorphotypes: SSH of the dissimilarity matrix of 114 species, based on characters related to locomotion (36 measurements, 62 coded characters); stress =0.15. Groups as identified in the hierarchical cluster analysis

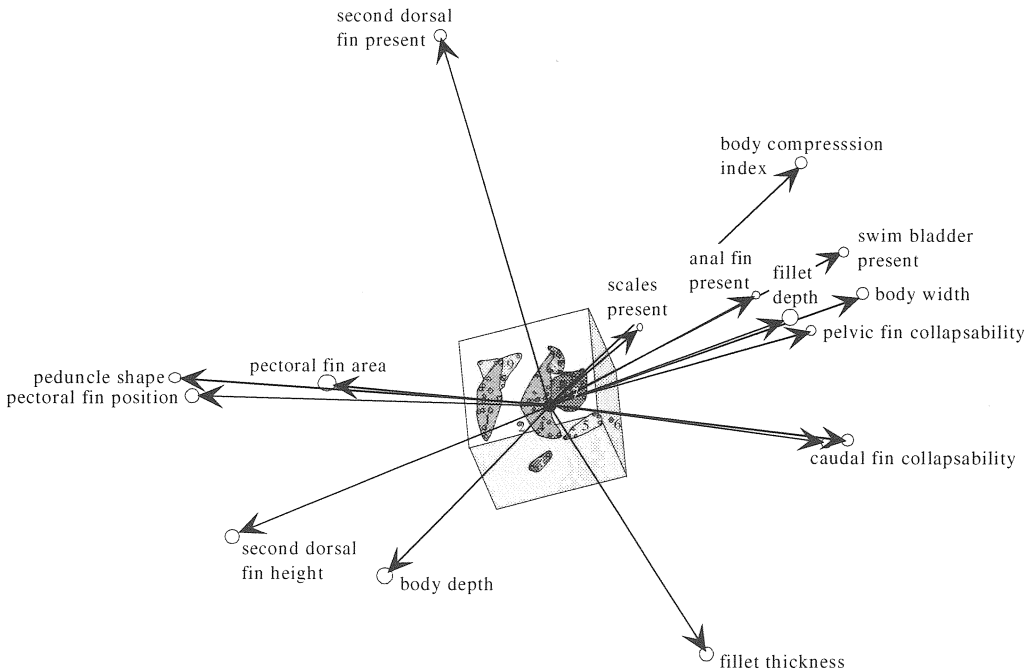


Figure 5.2.2.3 Intrinsic data PCC of the Locomotion Ecomorphotype SSH showing the direction of the best linear fit of characters with $|r| > 0.7$ in the ordination space, using unit vectors (circle size indicates the third dimension: large in the front, small in the back)

Feeding

We used 19 measurements and 33 coded characters (30 non-hierarchical, 5 primary and 17 secondary characters; Appendix 5) in the analysis of feeding ecomorphotypes. To avoid very low self-similarity values due to the relative rarity of vomerine, palatine and pterygoid teeth we aggregated the teeth data into mouth teeth (pre-maxillary, maxillary, dentary, vomerine, palatine and pterygoid teeth) and pharynx teeth (basiobranchial and pharyngeal teeth).

Again, a coarse level split into six rather phylogenetically driven groups (I –VI) can be observed at 0.585 dissimilarity in the cluster analysis (Figure 5.2.2.4). These groups are sharks (I), rays (II), *Gymnothorax parsinus* (III) and three distinct teleost groups: Macroramphosidae (V), a group composed of Monacanthidae, Aracanidae, Tetraodontidae and Diodontidae (IV) and the remaining teleosts (VI). Two possible finer-level splits were explored: the first at a dissimilarity of 0.488 splits the species into 8 groups, the second at 0.399 results in 18 groups. These splits define more clearly functional types. The 'eight-group-scenario' was used to define feeding ecomorphotypes. Groups 1 and 4 are composed of a series of families. Group 1 includes Triglidae, Zeidae, Carangidae, and other families; group 4 includes pleuronectiformes, Labridae, and Cheilodactylidae. Again, sharks (2) and rays (6), including *Callorhinchus milii*, form a group each, and *Gymnothorax parsinus* (3) separates out by itself. Group 5 is composed of Tetraodontidae, Diodontidae and Brachionichthydae; Macroramphosidae formed a group of their own (7), and finally Monacanthidae and Aracanidae (8) group together.

This 'eight-group-scenario' was confirmed in a relatively low stress (0.14) 3-d SSH (Figure 5.2.2.5), the species composition and body shape distribution within which are shown in Plate 3. Again PCC was used to identify the characters with high PCC correlation ($|r| > 0.7$), driving the direction of group-splits (Figure 5.2.2.6). Only one overall trend from the lower front to the top back of the ordination, from fishes with a large gape, protrusible jaws, a well-defined stomach and grasping or gripping teeth (group 1), toward fishes with a small gape, an undefined stomach, a long gut and shearing or crushing teeth (groups 5 and 8) is observed. We assigned feeding ecomorphotype numbers to the groups formed by the 0.488 level split roughly following this main split in the SSH-plot along the lower front to top back PCC axis.

A more detailed interpretation of the specific group characteristics was achieved by GST analysis of each group versus the remaining species. Fishes in group 1 (e.g. Triglidae, Zeidae, Carangidae) have numerous, long caeca, which translates to a large relative caecum length, rather rigid, long, bristly gill rakers, a large gape and gill slit, as well as a well developed lateralis system. Sharks (group 2) are defined by the lack of pharyngeal teeth, a long stomach (pharynx to pylorus distance), flexible and few gill rakers, large size, short jaws, inferior mouths and small gill slits. *G. parsinus* (group 3) is distinct here by its well developed sensory pores on the head, its large pharyngeal gape and relatively short head. Group 4 fish (e.g. pleuronectiformes, Labridae, and Cheilodactylidae) have well developed lips and pharyngeal teeth, few pyloric caeca, a short stomach and slightly protrusible mouths. For Tetraodontidae, Diodontidae and Brachionichthydae (group 5) a long gut, and absence of pyloric caeca and a lateralis system are distinctive; furthermore the former two have strong molariform mouth teeth and a short jaw. The rays and *C. milii* (group 6) are distinct amongst others by their numerous, small sensory pores all over their body, molariform, strong mouth and absent pharyngeal teeth, as well as by the presence of oral papillae, their small eyes and low HCI. Macroramphosidae (group 7) stand out due to their tubular snout; besides this, the lack of mouth teeth, the small

gape and the long head, due to the snout, all contribute to the separation of this group. Last but not least, group 8 (Monacanthidae and Aracanidae) is identified by the lack of pyloric caeca, a deep head, small gape area, and a relatively short upper jaw.

The general split observed in the SSH and PCC analyses is consistent with broad feeding guilds defined using qualitative dietary data from gut content analyses in the SEF project and literature: fishes at the bottom front of the ordination feed predominantly on other fishes and relatively soft, active crustaceans, whereas fishes at the top back feed predominantly on benthic infauna, colonial or hard-shelled (armoured) prey.

To test this qualitative dietary interpretation we performed a PCC analysis using extrinsic, quantitative stomach contents data on a separate SSH of a subset of 53 species for which appropriate diet data were available from the SEFEHS study (Figure 5.2.2.7). For this analysis we grouped the prey species on a functional basis into fish, cephalopods, pelagic active and pelagic passive invertebrates, benthic armoured and soft sessile invertebrates, benthic armoured and soft mobile invertebrates, infauna, and unknown components. This prey classification is designed to relate to the ecomorphology of the fishes under examination. In the interpretation of the overall ecomorphotypes, in a later section, we compared the feeding guilds observed in the SEFEHS, defined by prey type and location, to the ecomorphotypes defined by locomotion, feeding and self-preservation analyses.

Discussion

A strong phylogenetic pattern persisted in the groups of feeding ecomorphotypes. Closely related species are specialised – or evolutionary limited – to feed in broadly similar ways on similar suites of prey. Nevertheless, the groupings did reflect basic feeding modes described in the literature – biters, crushers, infaunal, ram and suction feeders (*sensu* Wootton 1992; Gerking 1994; Norton 1995). Similarly to the Locomotion analysis, these modes were used in naming the feeding ecomorphotypes.

'Biters' form group 8 (Monacanthidae and Aracanidae). These fish are characterised by incisiform teeth, small mouths and lacking stomachs (*sensu* Wootton 1992; Gerking 1994; Norton 1995). They feed primarily by biting pieces off attached prey like sponges, colonial ascidians and bryozoans.

Group 5 (Tetraodontidae and Diodontidae) are 'crushers/biters', using their large molariform teeth in the jaws to crush molluscs and the shells of hermit crabs (*sensu* Wootton 1992; Gerking 1994). The Brachionichthydae *Brachionichthys sp.2* surprisingly also falls into this group. This fish appears to be an ambush predator, gulping its prey whole (Green, CSIRO pers. comment). It was grouped into this feeding type by its gut structure and underdeveloped lateralis system; however, it is an outlier of the group in the cluster analysis.

The Macroramphosidae (group 7 – 'probers') have a highly specialised feeding apparatus and therefore mode: they are probers, picking small crustacea from substrate and possibly crevices using their long thin snouts (Gerking 1994).

Benthic infauna and crustacea feeders were represented by two distinct clusters. The rays (group 6 – 'benthic infaunal feeder/crusher') have relatively small mouths that open and/or protrude ventrally and the dentition consists of molariform plates. The teleost group (group 4 – 'infaunal feeders/crushers') is more diverse. It includes pleuronectiformes, *Synchiropus*

calauropomus, and other bottom associated infaunal feeders with ventrally protruding mouths and indistinct dentition. However, it also contains Labridae and Cheilodactylidae, which are pickers and crushers (*sensu* Wootton 1992; Gerking 1994), that use their large lips to pick and test food and their molariform pharyngeal teeth to crush shells, ophiuroids and bryozoans.

Ram feeders with a large gape and grasping teeth, cuspid or canine, are represented by two groups: the sharks (group 2 – 'ram feeder (shark)') and *G. parsinus* (group 3 – 'ram feeder (eel)'). The former group is known to feed primarily on fish and cephalopods, with the exception of the two Pristiophoridae – an outlier pair in the cluster analysis – which are infaunal crustacea feeders. No dietary data was available for *G.parsinus*.

The last group (group 1 – 'pelagic/demersal suction/ram feeders') is composed of a collection of pelagic and demersal ram and suction feeders. They have grasping or biting teeth, similar to the general ram feeders above, but these range from small villiform types to large canines. The fish in this group feed on fish and crustacea. At the lower level, this group may be separated mainly by feeding area and mode, from pelagic (Carangidae, Centrolophidae, Zeidae, etc.) and demersal (Moridae, Platycephalidae, Scorpaenidae, Uranoscopidae, etc.) suction or ram feeders (*sensu* Gerking 1994; Norton 1995) to demersal pickers or scoopers (Triglidae) (*sensu* Gerking 1994).

Similarly to the locomotion analysis, elasmobranchs and teleosts show corresponding feeding types. The ram and ram/suction feeders (groups 1, 2 and 3), and the infaunal feeders/crushers (groups 4 and 6). However, the distinction in the functional morphology is more clearly drawn in the feeding types.

Although the trends in the SSH of feeding ecomorphotype and diet preference can be matched up, cluster analyses based on diet returned rather different groups of fishes to the ecomorphology analysis. This may be explained by the fact that the morphology reflects the functional type of prey that can be successfully captured and the foraging methods that are employed, rather than prey species. We tried to accommodate for this difference by also classifying the prey into functional groups. However, since little was known of the particular prey species' ecology and often prey could not be identified beyond order or family, this approach was of limited success. Nevertheless, as seen in the PCC of diet on the species SSH (Figure 5.2.2.7), trends that are supported especially by the dentition and gut-structure could be identified.

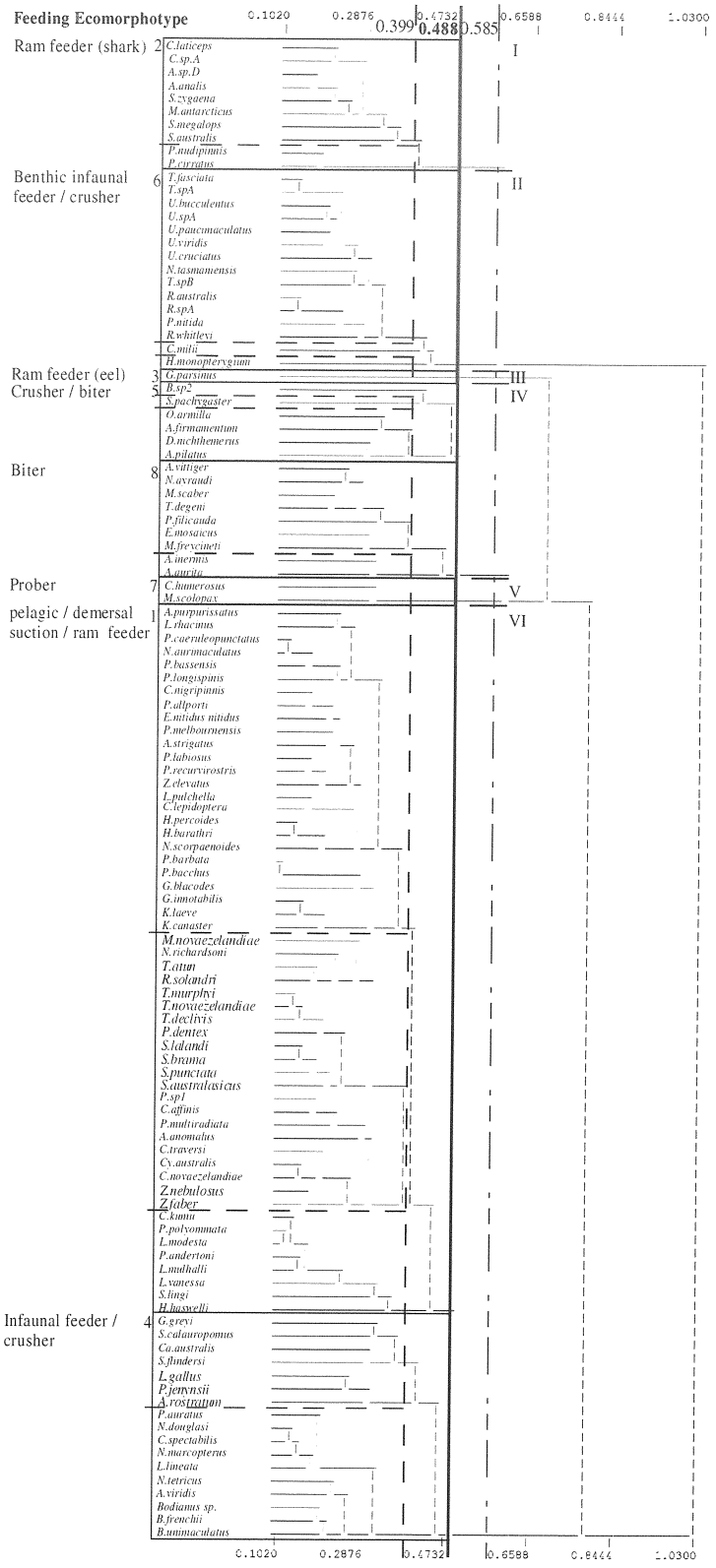


Figure 5.2.2.4 Agglomerative cluster analysis of the dissimilarity matrix of 114 species, based on characters related to feeding (19 measurements, 33 coded characters). Groups indicated: I-VI split-off level =0.585; 1-8 split-off level =0.488 dissimilarity

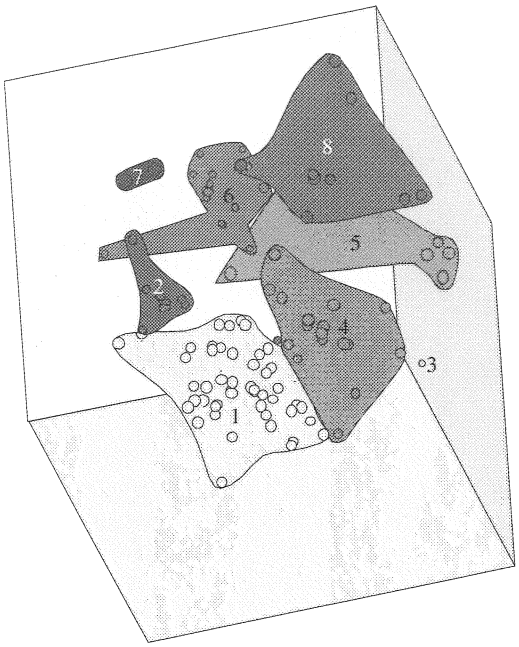
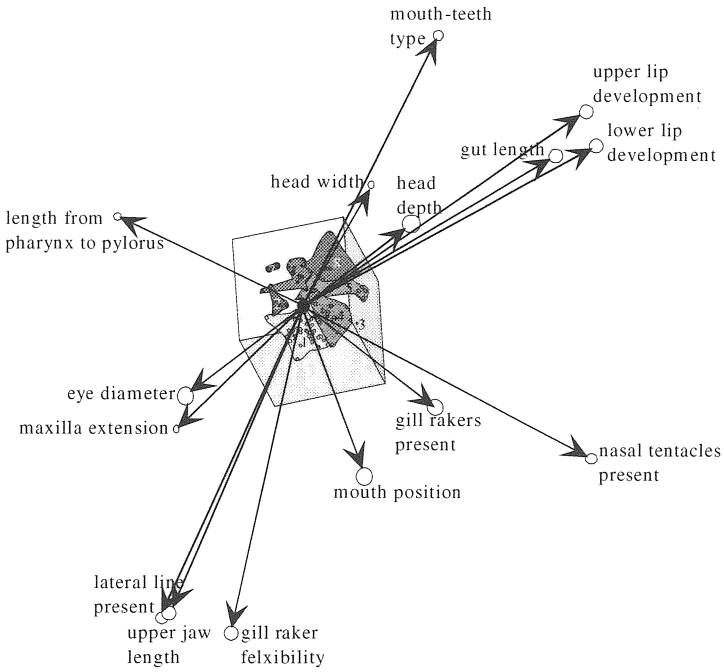


Figure 5.2.2.5 Feeding Ecomorphotypes: SSH of the dissimilarity matrix of 114 species, based on characters related to feeding (19 measurements, 33 coded characters);



stress =0.14. Groups as identified in the hierarchical cluster analysis

Figure 5.2.2.6 Intrinsic data PCC of the Feeding Ecomorphotype SSH showing the direction of the best linear fit of characters with $|r| > 0.7$ in the ordination space, using unit vectors (circle size indicates the third dimension: large in the front, small in the back)

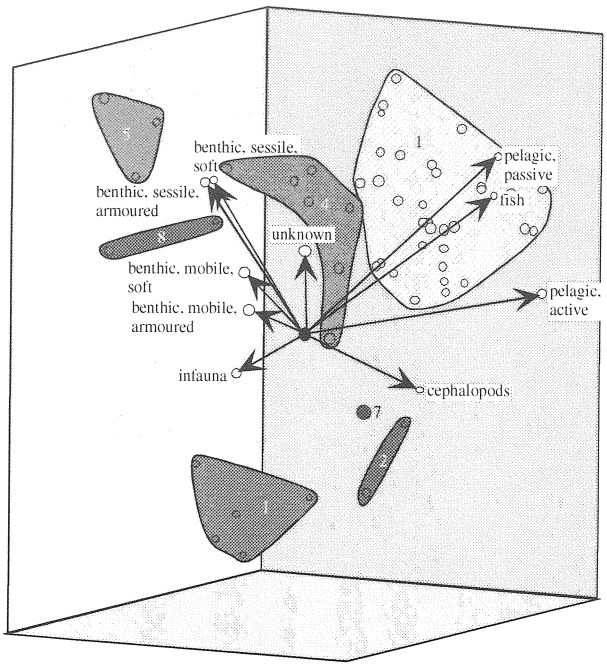


Figure 5.2.2.7 PCC analysis of extrinsic diet data overlaying an SSH ordination of a subset of 53 species for which quantitative diet data were available from the SEFEHS, based on characters related to feeding (19 measurements, 33 coded characters); stress =0.14; groups and numbers as identified in the overall feeding analysis

Self-preservation

Locomotion forms an integral part of predator avoidance, as it depends on the locomotion type if a fish can rely on 'out-running' a predator, or if it has to resort to other techniques to defend itself. Hence, two separate approaches or the analysis of self-preservation ecomorphotypes were explored: (a) self-preservation (excluding locomotion) and (b) self-preservation (including locomotion). Again, the analyses were applied to all species (one fish, each).

(a) Self-preservation (excluding locomotion)

The character-set for this analysis was composed of 8 measurements, 26 coded characters (16 non-hierarchical, 5 hierarchical primary, 13 hierarchical secondary characters; Appendix 5). The cluster analysis resulted in a 6 group split at 0.603 dissimilarity (Figure 5.2.2.8). The groups, however, were not as well defined as in the other analyses, which was confirmed by the large stress (0.21) of the 3-d SSH (Figure 5.2.2.9). Interpretation of the ordination by PCC identified the main gradients (Figure 5.2.2.10); from the bottom front to the top back (increasing body depth and BCI) and a left to right trend (increasing colour patterning of the body, scale size and eye diameter as opposed to decreasing development of the lateral line). Scale presence and absence, as well as specialisation also plays a part in the group separation. Plate 4 shows the species composition and shape distribution within these groups.

Due to the high stress and low group definition in the SSH we abandoned approach (a) at this stage.

(b) Self-preservation (including locomotion)

We repeated the analysis including locomotion characters related to acceleration, top speed and manoeuvrability. This resulted in a character increase to 26 measurements and 40 coded characters (20 non-hierarchical, 10 hierarchical primary, 36 hierarchical secondary characters; Appendix 5). There were few changes in the groupings at the same dissimilarity level (0.603): 7 instead of 6 groups split off at this level, and some species changed group affiliation (Figure 5.2.2.11 and Plate 5). Similar to analysis (a), *Gymnothorax parsinus* formed its own group (1); the rays group together (2); group 4 consists of a combination of 'sustained swimmers' Carangidae, Centrolophidae, etc., sharks, and the 'burst swimmers' Merlucciidae and Macrouridae. Group 6 was composed of Monacanthidae, Zeidae and Macroramphosidae. Aracanidae, Diodontidae and Tetraodontidae formed group 7; and a large general teleost group (5) contained all the other species. The new group in this analysis in comparison to (a) is composed of the pleuronectiformes (group 3). Species that changed group when locomotion characters were included are: *Squatina australis*, *Sillago flindersi*, *Pempheris multiradiatus* and *Brachionichthys sp.2*; they all joined the largest teleost group (5).

The SSH of this analysis defined the groupings more clearly (stress=0.15; Figure 5.2.2.12). The PCC analysis identified the characters (correlation of $|r|>0.7$) governing the main splits in the ordination plot (Figure 5.2.2.13). From the rear left towards the front right (decreasing area and increasingly central attachment of the pectoral fin), left to right (increasing peduncle depth), top left to bottom (decreasing height of the second dorsal fin and BCI), and central back to front (decreasing body width). Each of the groups were numbered for the distinction of ecomorphotypes (Figure 5.2.2.12), according to the direction of the main split in the SSH-plot (rear left to front right).

The characteristic features of each group were identified by GST analysis of each group against the remaining species. *G.parsinus* (group 1) stands out by the lack of lateral fins, the elongate body shape, and therefore narrow width, well developed sensory pores on the head, and the long-based dorsal fin. The rays (group 2) are characterised by the presence of oral papillae, the numerous, small sensory pores on their body, the absence of scales, specialised position of the pectoral fins, and the low BCI. Pleuronectiformes (group 3) are distinct due to the base length of their functional pectoral fins, the functional absence of median and pelvic fins, and due to their low body depth and BCI. Group 4 (Carangidae, Centrolophidae, sharks, etc.) fish have long bodies of a relatively narrow width, numerous sensory pores on head and body, a rounded peduncle, well developed lateralis system, lateral, small eyes and lack of patterning of the body. Group 5 fish (among others Triglidae, Scorpinidae, Moridae, Labridae), on the other hand, are characterised by large areas of anal and first dorsal fins, long-based pectoral and first dorsal fins, wide ventral surfaces (pelvic base width), well developed lateralis system and abdominal musculature, as well as large eyes. Zeidae, Macroramphosidae and Monacanthidae (group 6) have compressed, deep bodies (high BCI), small pectoral and pelvic fins, few, though well developed sensory pores on the head, narrowly keeled bodies (low pelvic body width), first dorsal fins of small area – often reduced to a spine, and very thin abdominal walls. Finally group 7 (Aracanidae, Diodontidae and Tetraodontidae) are characterised by the lack of a lateralis system, pelvic and second dorsal fins, as well as by the back-set anal fins, the central positioning of the pectoral fins, and the large, modified scales.

Discussion

Self-preservation ecomorphotypes are broadly based on overall body shape with some underlying factors of scale modification, and development of the lateralis system. The inclusion of locomotion characters did not essentially change the groupings, despite the range of additional characters. However, it did cluster the groups more tightly, and it resulted in the inclusion of dorsal fin (spine) height, another important character for the group distinction.

Interpretation of the self-preservation ecomorphotypes identified in this analysis is difficult. Unlike locomotion and feeding, self-preservation, as a function of morphological characters, is not well documented or described in the literature. Furthermore, several potentially important characters for this functional area were not recorded; for example the presence of interlocking fin spines, head spination and the presence of poison glands should be included in future studies. In addition, predator avoidance and defence mechanisms are difficult to measure using only morphology – behaviours, such as hiding, burrowing, schooling and scare tactics, as well as chemical predator deterrents play a great part in this ecological function. It is impossible to include any of these behaviours in the current study as firstly, ecomorphology is defined as the relation between ecology and morphology, explicitly excluding behaviour, and, secondly, it is not feasible to observe each of the 114 species behave in its environment.

We did not attempt to name the ecomorphotypes, as there are no basic 'self-preservation modes' that are generally accepted. However, we interpreted the self-preservation types based on the possible functions of their distinctive characteristics, in combination with known behavioural attributes of their members.

G. parsinus (group 1) has a long, snake-like body without appendages, enabling it to hide in small holes in highly structured habitats or even burrow in the sediments (*sensu* Whitehead 1975).

Groups 2 (rays) and 3 (pleuronectiformes) are both dorso-ventrally (functional definition of dorso-ventral for the latter) flattened. They can be described as hiders that lie on flat bottom, or partially bury themselves in the sediment (*sensu* Whitehead 1975).

Group 4 is comprised of large bodied 'sustained swimmers' (locomotion groups 8 and 9) and two burst swimmers, both of which are slope rather than shelf species (*Macruronus novaezelandiae* and *Caelorinchus australis*). Their defense mechanism is most likely composed of a combination of early detection of predators (highly developed sensory system – Alexander 1967 and Jobling 1995), and escaping an attack (fast, sustained swimmers), besides being simply too large to be eaten (*sensu* Whitehead 1975).

Group 6 combines Zeidae, Monacanthidae and Macroramphosidae, all of which are extremely laterally compressed, and all of which have a relatively high dorsal fin of small area. However, while the Zeidae use their sharply keeled body and silvery colour to be camouflaged in the watercolumn (Whitehead 1975), Monacanthidae use their narrow body shape and colouring for hiding in crevices of structural habitat. The most obvious defense mechanism of the Macroramphosidae is their enlarged, rigid dorsal spine (*sensu* Jobling 1995).

Group 7 fishes either use their armouring – bony scale casing in Aracanidae, large spines in Diodontidae (Whitehead 1975 and Jobling 1995) – and/or a behaviour of inflating their body to a sphere (Diodontidae and Tetraodontidae) to deter potential predators (Whitehead 1975).

For fishes in group 5 no common, distinctive defense mechanism could be identified from the characters recorded in the present study.

Considering these group descriptions, some weaknesses of the analysis become apparent. For example, group 6 fishes show two or even three self-preservation mechanisms, although all of these rely on the same morphological features. Group 7 on the other hand is composed of heavily armoured fish with bony scales (Aracanidae), as well as fish that have virtually no scales and only use the behaviour of inflation to deter predation (Tetraodontidae). Group 5 is difficult to categorise in terms of self-preservation, due to the wide range of species comprising the group. However, the compositions of groups 1 to 4 were consistent within themselves and they could be described in self-preservation terms.

Despite the inadequacy of our self-preservation analysis, and the lack of some potentially important characters, the analysis of this functional area identified some deficiencies in the characters measured (despite our 'shotgun approach') that can be addressed in future studies. It also provides a third dimension to the overall ecomorphotype analysis.

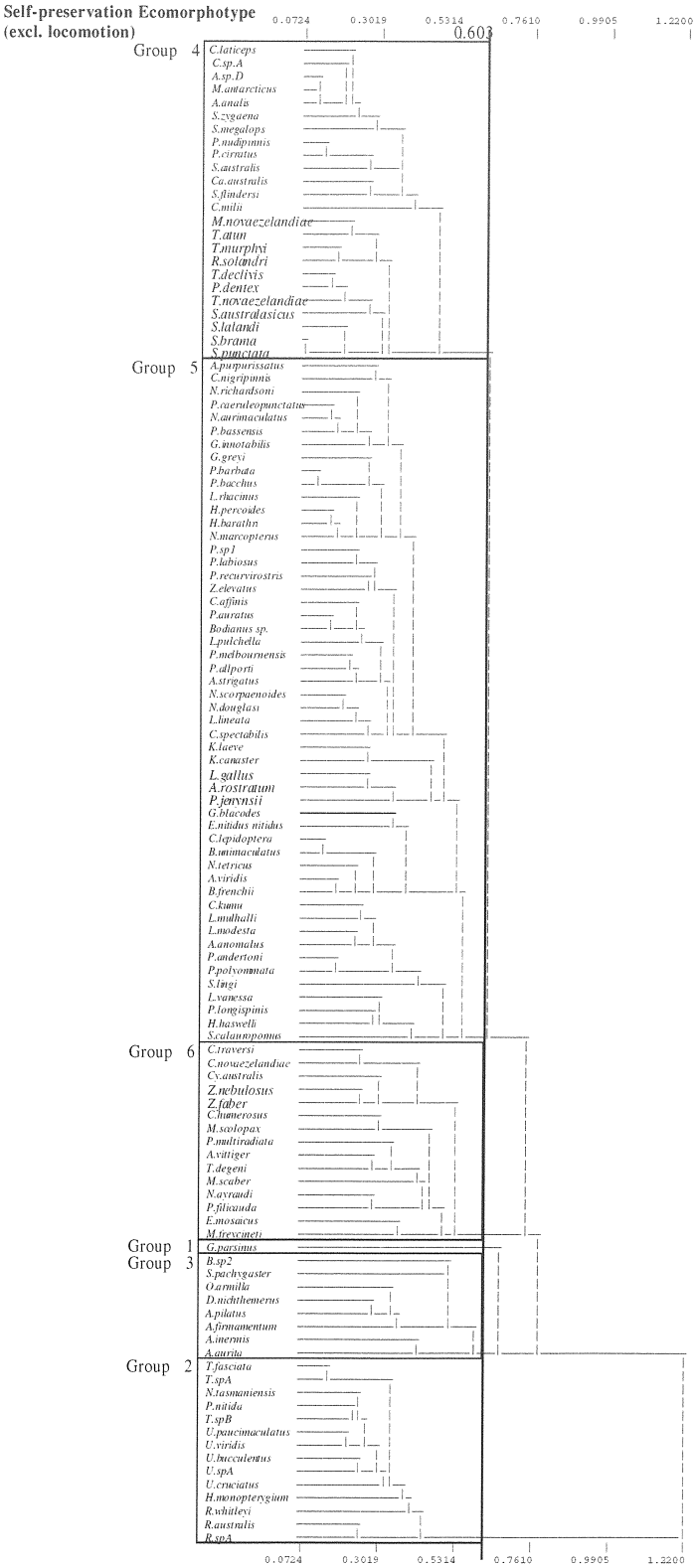


Figure 5.2.2.8 Agglomerative cluster analysis of the dissimilarity matrix of 114 species, based on characters related to defence and predator avoidance functions (excluding locomotion) (8 measurements, 26 coded characters). Groups indicated: 1-6 split-off level =0.603 dissimilarity

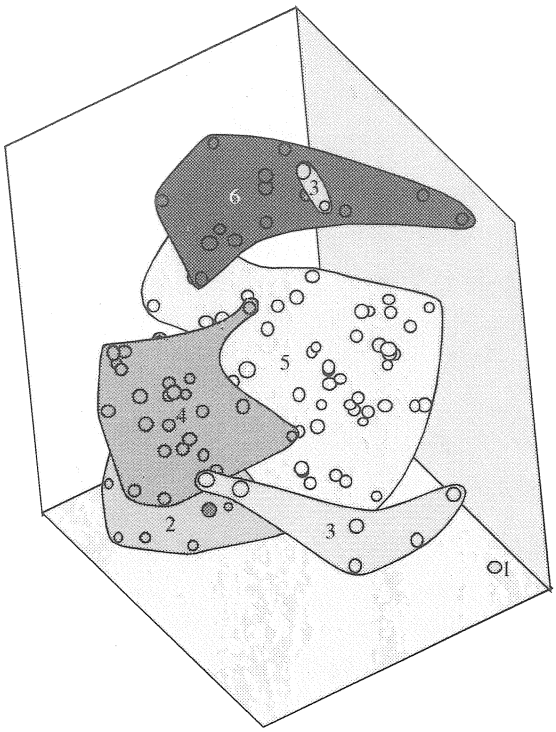


Figure 5.2.2.9 Self-Preservation (excl. locomotion) Ecomorphotypes: SSH of the dissimilarity matrix of 114 species, based on characters related to defence and predator avoidance functions (excluding locomotion) (8 measurements, 26 coded characters); stress =0.21. Groups as identified in the hierarchical cluster analysis

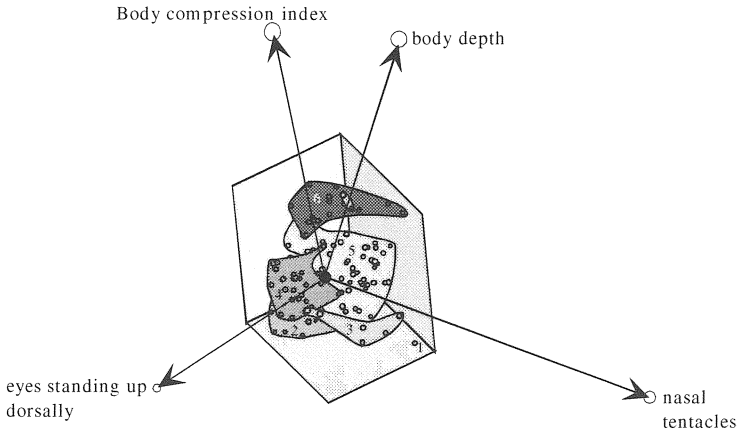


Figure 5.2.1.10 Intrinsic data PCC of the Self-Preservation (excl. locomotion) Ecomorphotype SSH showing the direction of the best linear fit of characters with $|r| > 0.7$ in the ordination space, using unit vectors (circle size indicates the third dimension: large in the front, small in the back)

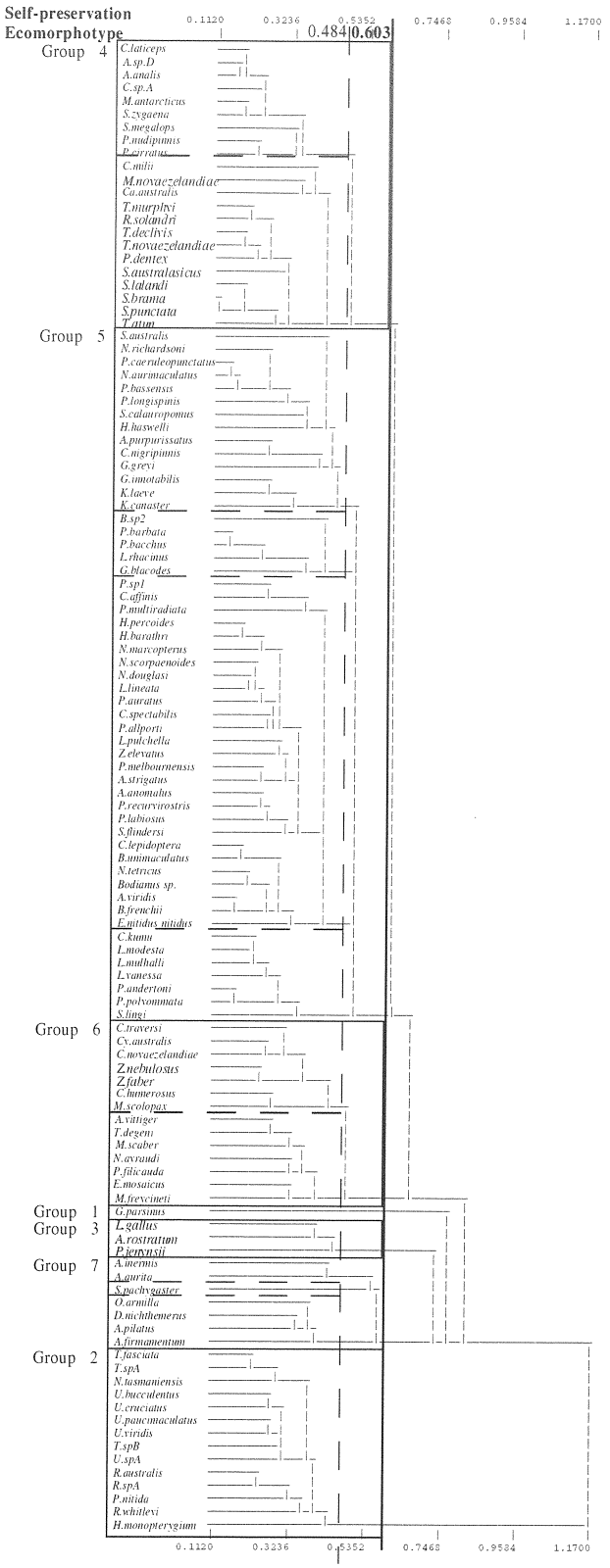


Figure 5.2.2.11 Agglomerative cluster analysis of the dissimilarity matrix of 114 species, based on characters related to defence and predator avoidance functions (including locomotion) (26 measurements, 40 coded characters). Groups indicated: 1-7 split-off level =0.603 dissimilarity

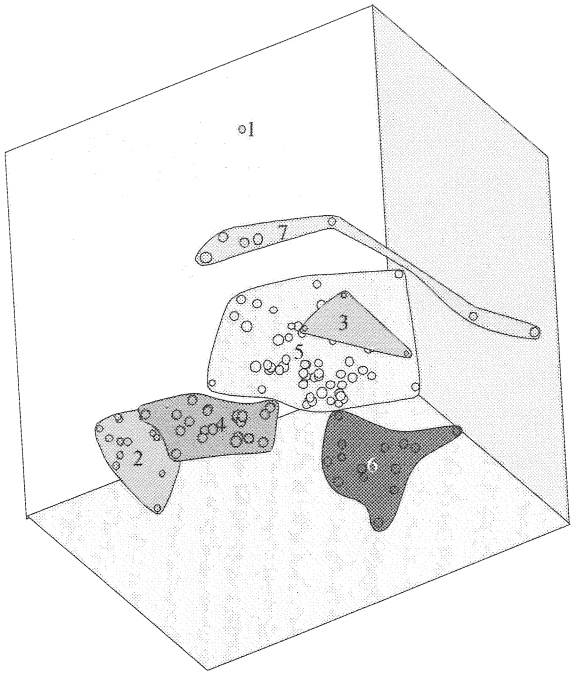


Figure 5.2.2.12 Self-Preservation Ecomorphotypes: SSH of the dissimilarity matrix of 114 species, based on characters related to defence and predator avoidance functions (including locomotion) (26 measurements, 40 coded characters); stress =0.15. Groups as identified in the hierarchical cluster analysis

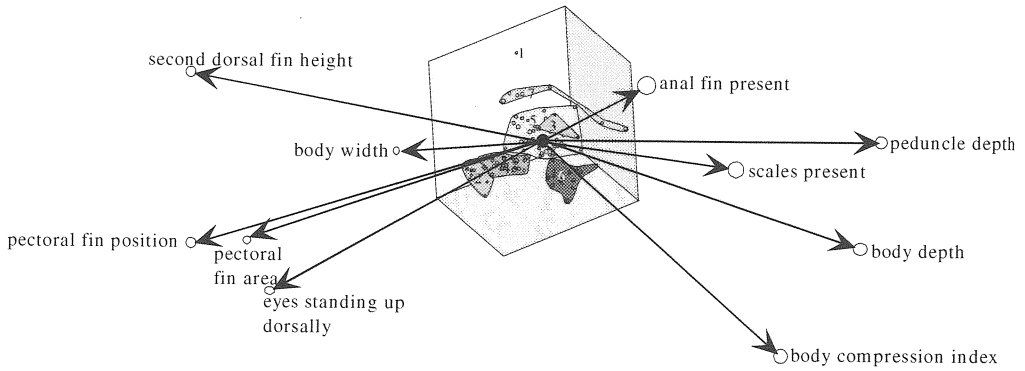


Figure 5.2.1.13 Intrinsic data PCC of the Self-Preservation Ecomorphotype SSH showing the direction of the best linear fit of characters with $|r| > 0.7$ in the ordination space, using unit vectors (circle size indicates the third dimension: large in the front, small in the back)

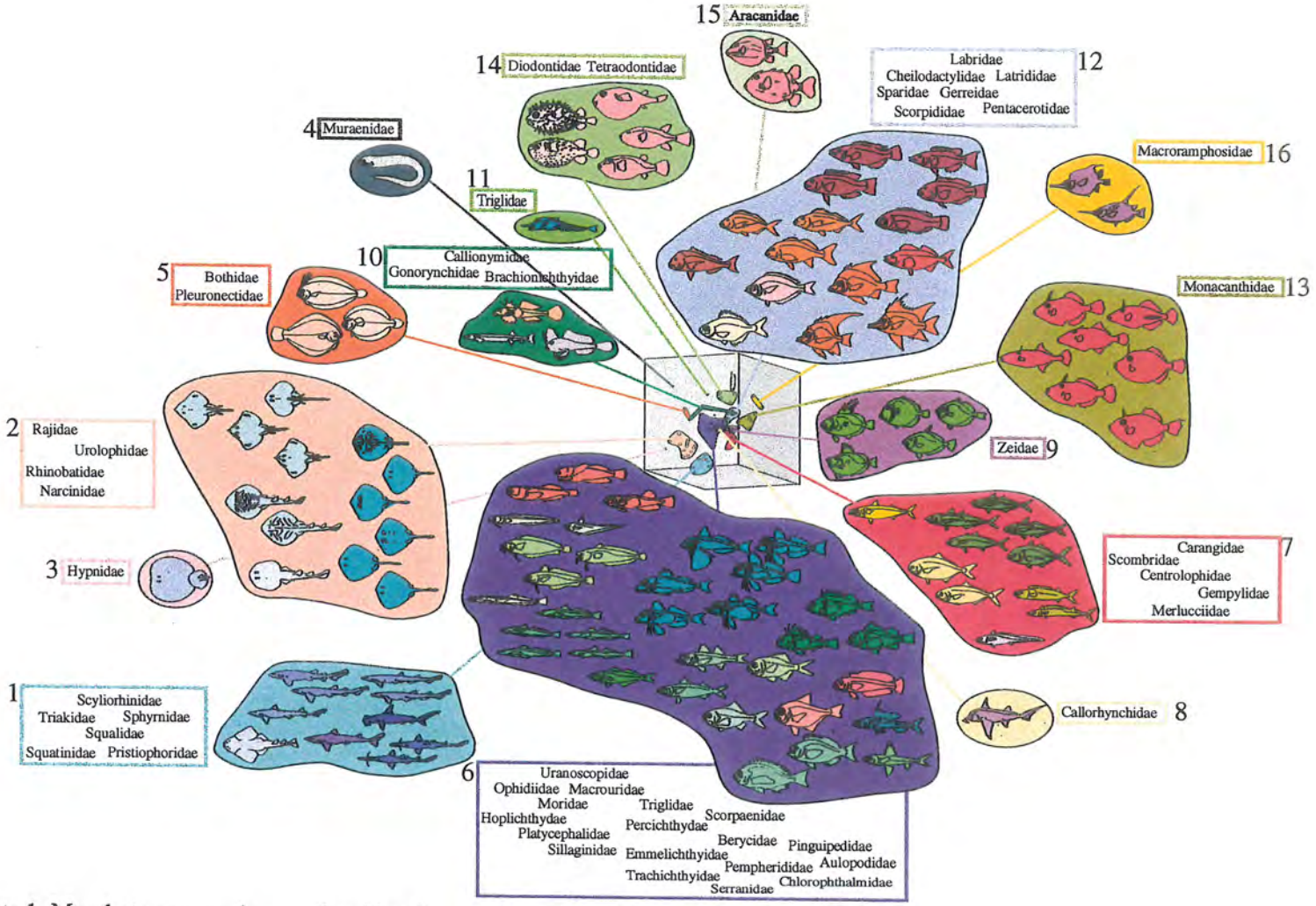


Plate 1 Morphotypes: species membership of groups formed by SSH ordination (Figure 5.2.1.2), based on all characters measured (dis-similarity level = 0.443). Fish colour shows family membership, background colour shows morphotype

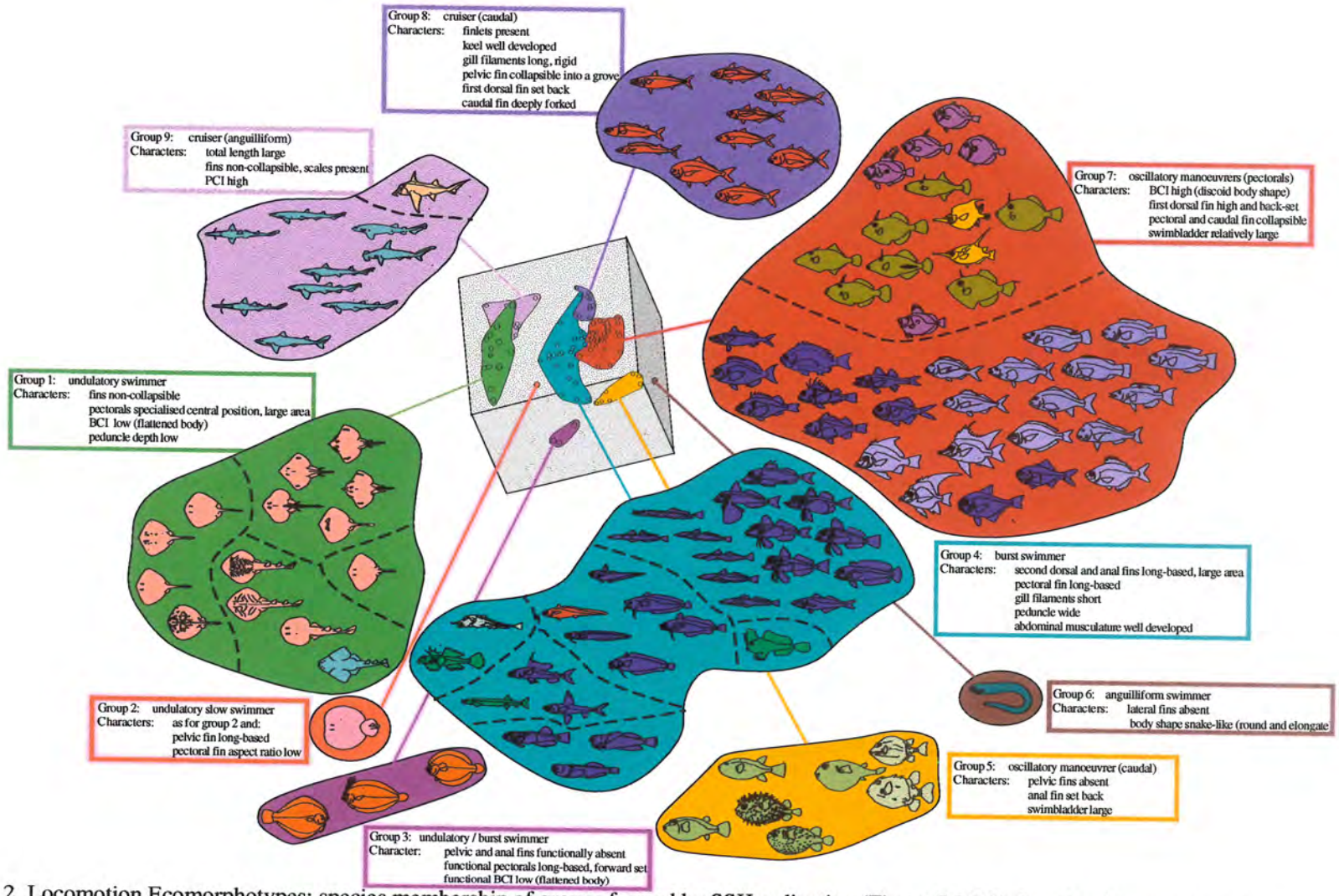


Plate 2 Locomotion Ecomorphotypes: species membership of groups formed by SSH ordination (Figure 5.2.2.2), based on locomotion related characters (dis-similarity level = 0.512). Fish colour shows morphotype, background colour shows locomotion ecomorphotype; group characters as identified in GSTA

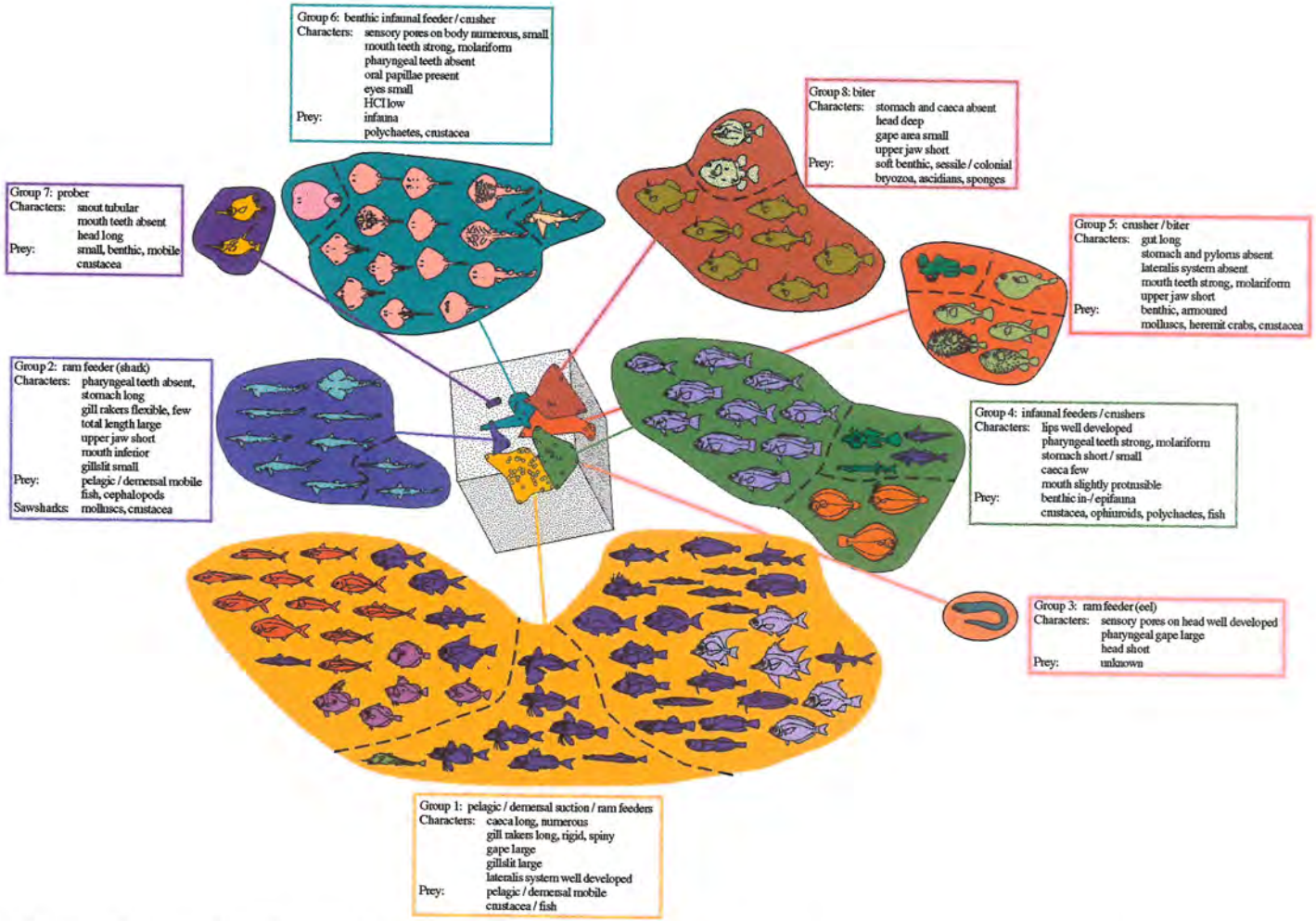


Plate 3 Feeding Ecomorphotypes: dspecies membership of groups formed by SSH ordination (Figure 5.2.2.5), based on feeding related characters (dissimilarity level = 0.488). Fish colour shows morphotype, background colour shows feeding ecomorphotype; group characters as identified in GSTA, prey type generalised from SEF data and literature

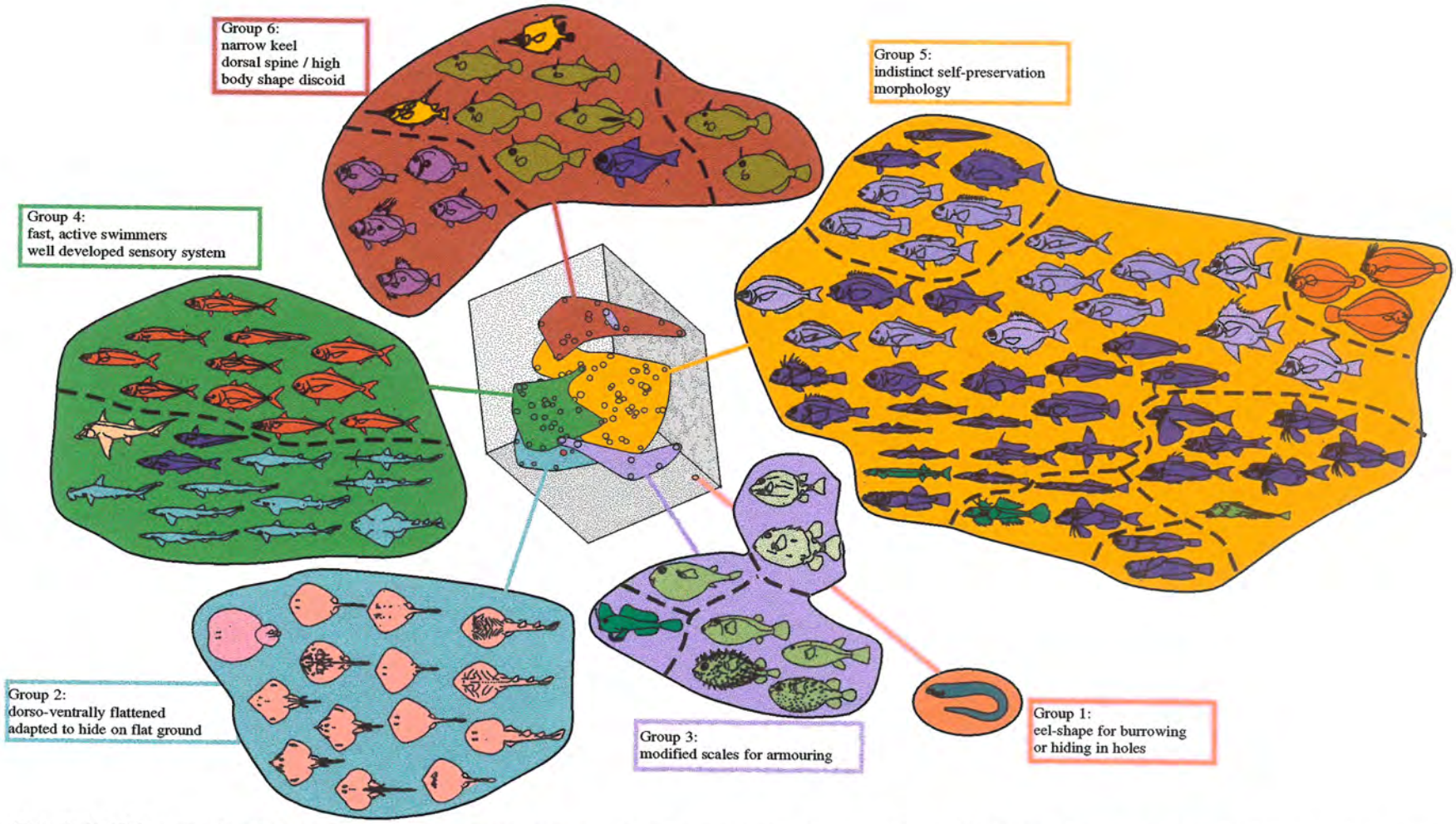


Plate 4 Self-Preservation (excl. locomotion) Ecomorphotypes: species membership of groups formed by SSH ordination (Figure 5.2.2.9), based on self-preservation (excl. locomotion) related characters (dis-similarity level = 0.603). Fish colour shows morphotype, background colour shows self-preservation (excl. locomotion)

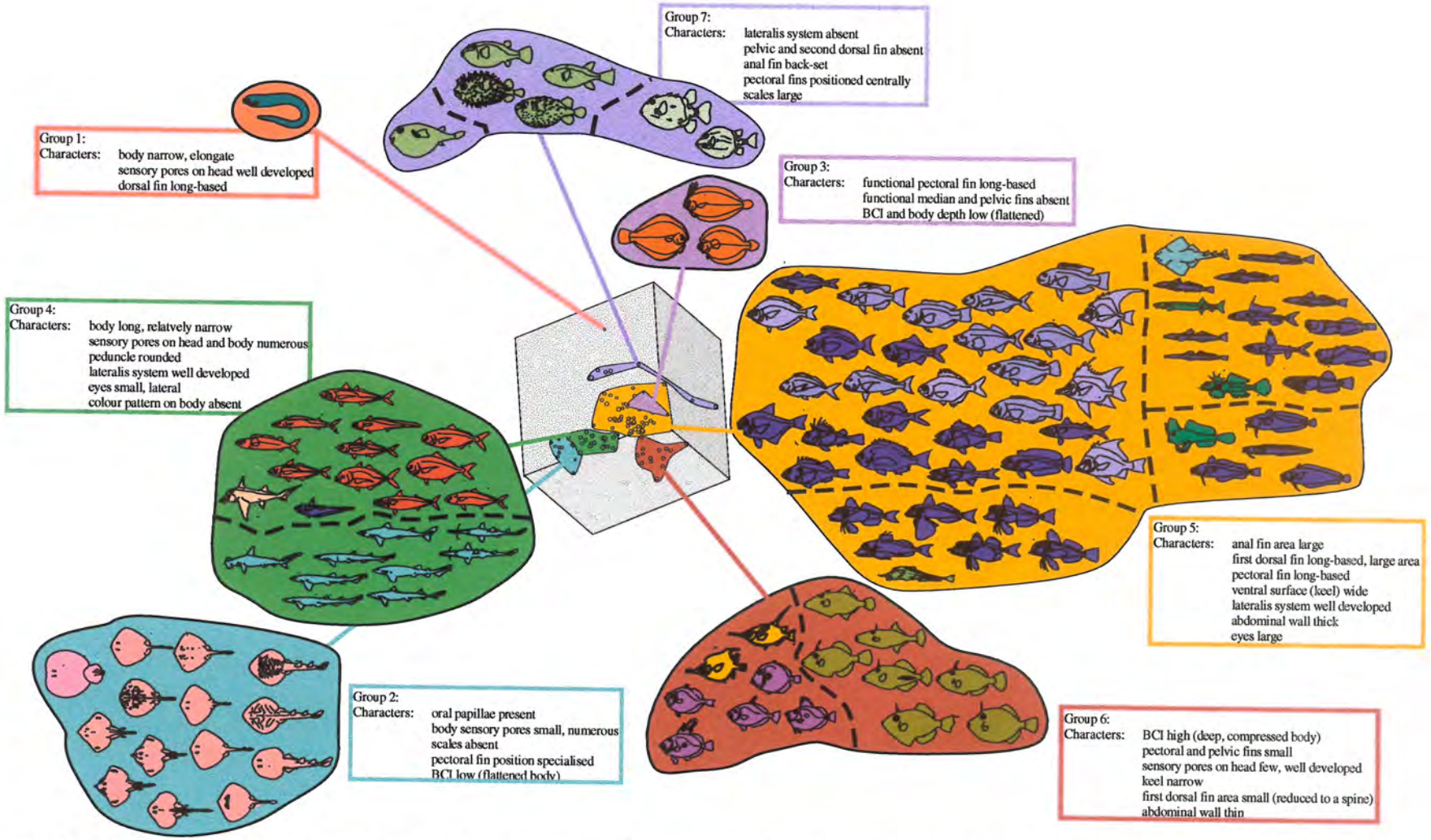


Plate 5 Self-Preservation Ecomorphotypes: species membership of groups formed by SSH ordination (Figure 5.2.2.12), based on self-preservation (incl. locomotion) related characters (dis-similarity level = 0.0.603). Fish colour shows morphotype, background colour shows self-preservation ecomorphotype; group characters as identified in GSTA

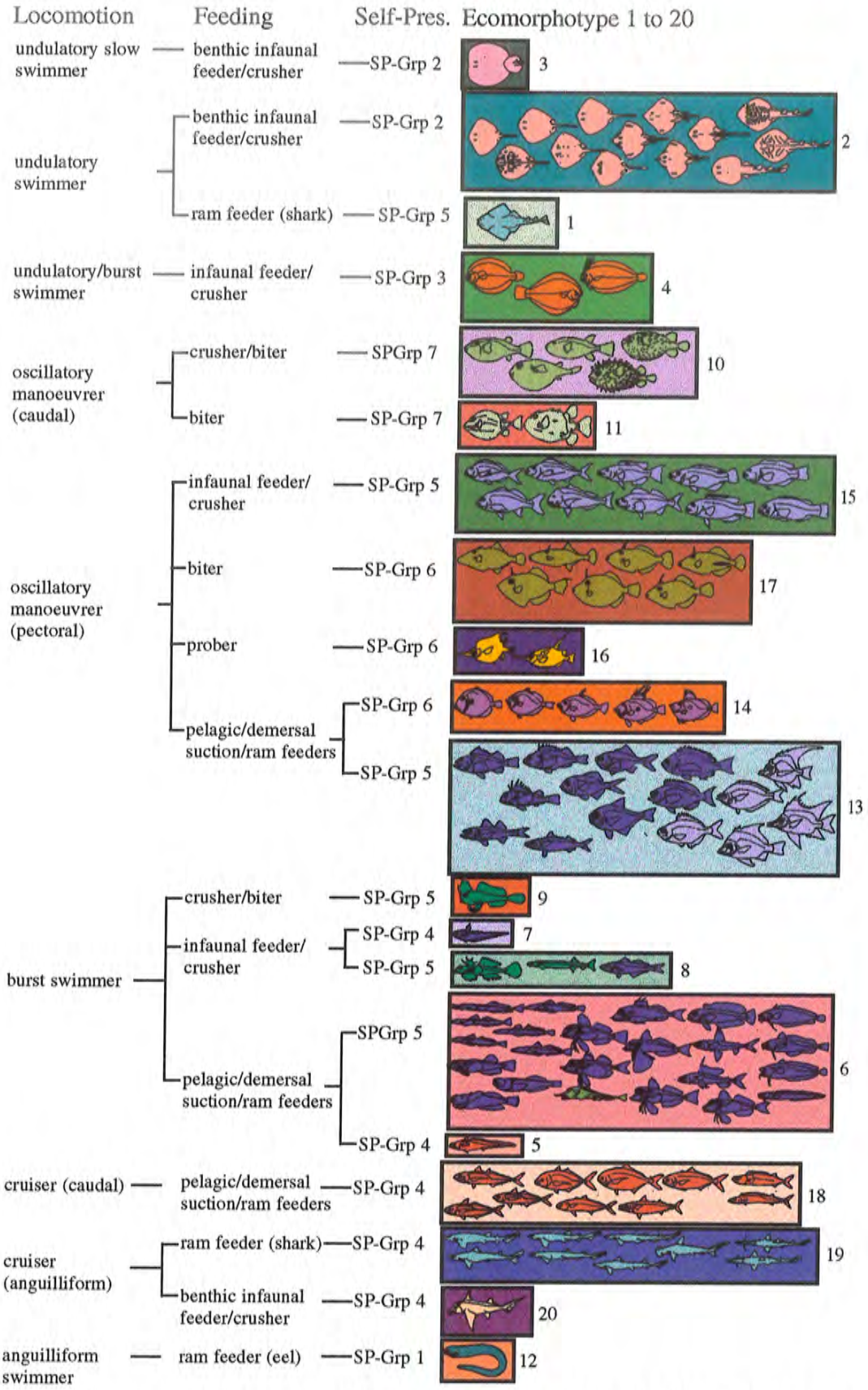


Plate 6 Ecomorphotype Groups: fish species associated with the 20 ecomorphotypes (numbered) defined from the Locomotion, Feeding and Self-Preservation analyses; fish colour shows morphotype, background colour ecomorphotype

Ecomorphotypes

In order to integrate across the three eco-functional areas of locomotion, feeding and self-preservation, we assigned a number to each group in the three analyses according to the main split in the SSH ordination plot. By these means we identified 20 ecomorphotypes based on the 9 locomotion, 8 feeding and 7 self-preservation types (Figure 5.2.2.14 and Plate 6).

Surprisingly the groupings correspond closely to the ones observed in the morphotype analysis. While the most morphologically distinct families (Zeidae (14), Monacanthidae (17), Macroramphosidae (16), Diodontidae and Tetraodontidae (10), Aracanidae (11), rays (2), and pleuronectiformes (4)) remained in identical groups, there were some minor change in the shark group and the Carangidae/Centrolophidae group, and considerable change in the more general family groups. *Squatina australis* (1) was separated from the other sharks (19) by its locomotion and self-preservation type; *Macruronus novaezelandiae* (5) belonged to a separate locomotion type from the fish in group 18; *Brachionichthys sp.2* (9) differed in both, locomotion and feeding type from its co-morphotypes *Synchiropus calauropomus* and *Gonorynchus greyi* (8), which were joined by *Sillago flindersi*. The two most diverse morphotype groups were recombined into three groups: they separated by locomotion type into the elongate, dorso-ventrally flattened (6), and the laterally compressed, shorter fishes; the latter split further by feeding type into fish with strong teeth in jaw and pharynx, and poorly defined stomach (15), and fish with small grasping teeth, large gape and well defined stomach (10). *Gymnothorax parsinus* (12), *Hypnos monopterygium* (3), *Callorhinchus milii* (20), and *Caelorinchus australis* (13) each represents a separate ecomorphotype.

As mentioned above, the self-preservation ecomorphotypes identified here need to be viewed cautiously. Many characters of potential importance were not included in the data collection, and the groups formed, though to some extent reflecting possible self-preservation methods, are unclear. Only minor changes in the group distribution are observed if self-preservation is excluded; the 20 ecomorphotypes discussed above condense into 17. In two cases a single species group, *M. novaezelandiae* (5) and *C. australis* (7), joins a larger group – 6 and 8 respectively; the third case of amalgamation joins the Zeidae (group 14) to group 13.

Despite the uncertainty of the self-preservation ecomorphotypes, we continue to consider the 20 ecomorphotypes identified from all three functional analyses. Two of the three extra groups are single species groups representing slope, rather than shelf species, therefore presenting a 'special case'. The third extra group, the Zeidae, has a narrowly keeled, silvery body that clearly functions to camouflage the fish in the watercolumn -- a self-preservation property that differentiates this family from the other group 13 fish.

Discussion

Morphotypes and ecomorphotypes, as defined by the three analyses, correspond well; this supports the notion that, while species adapt to their environment, they are also limited by past evolutionary adaptions in the environments they can inhabit. Furthermore, taxonomy relies heavily on fin and body features that also have a strong functional significance. However, these groups were identified in rather rigid, two-dimensional analyses (hierarchical cluster analyses), and the self-preservation ecomorphotypes identified were limited by the character-set.

Sub-structure within ecomorphotypes was not well identified because of the scope of our study that compared species of 53 families. Targeted analyses would be required to show functional groupings within ecomorphotypes.

Our results show that, at a very broad level of community interaction, phylogeny at class level does not reflect functionality; however at the family level, taxonomy corresponds well to the locomotion style, feeding and possibly self-preservation ecology. This shows that ecomorphology is a useful tool to identify functionality over phylogeny, although, its power to differentiate functional groups depends on the taxonomic spread of the species in the analysis. Still, as we have knowingly ignored the statistical problem of species as samples (they are not independent, due to their evolutionary relationships), it would be very interesting to repeat the analyses using a correction factor for the phylogeny as suggested by Felsenstein (1985), once the cladistic relationships between the species is determined.

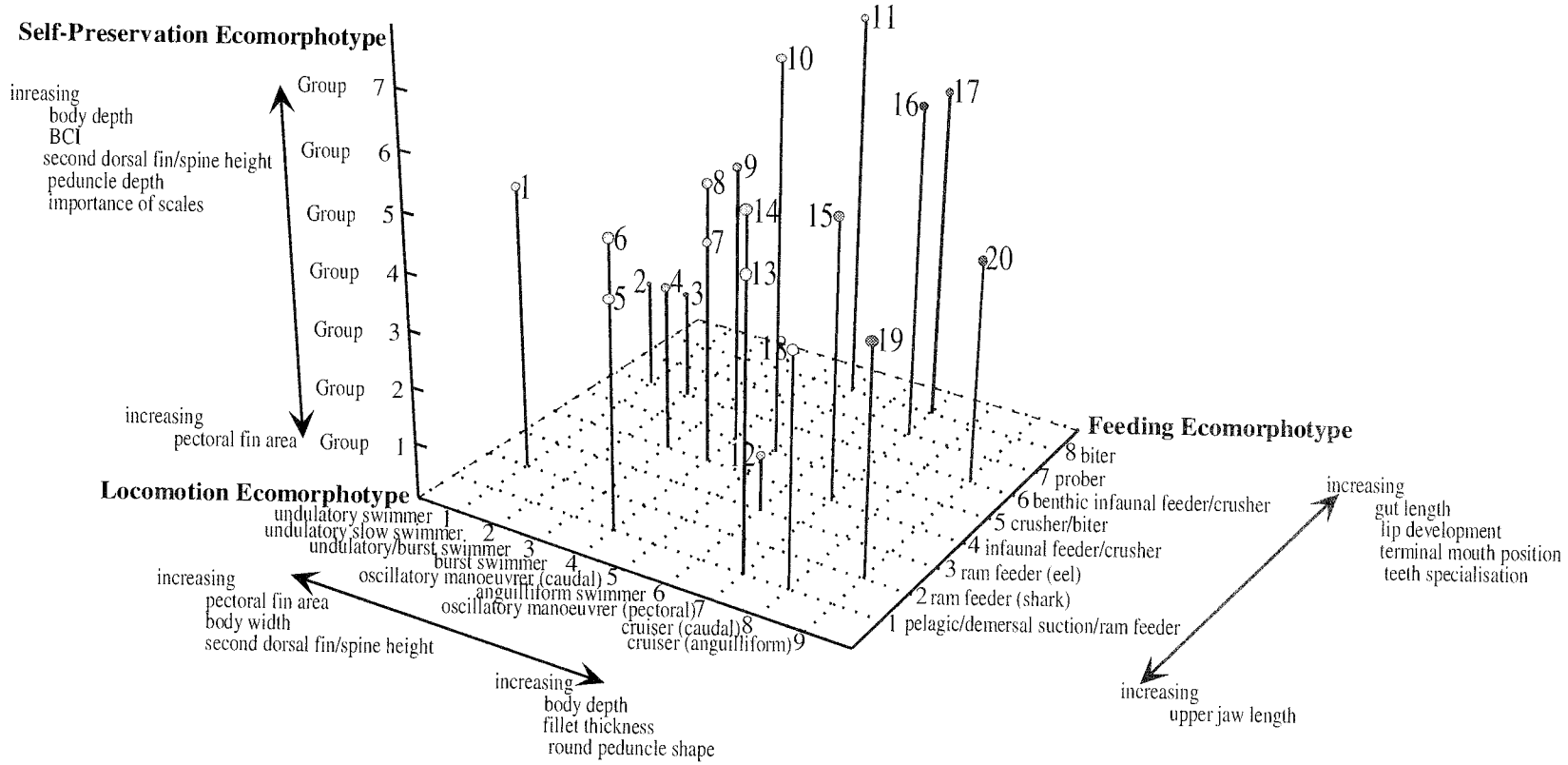


Figure 5.2.1.14 Ecomorphotypesummary figure, showing the fish group distribution defined by combination of the Locomotion, Feeding and Self-Preservation analyses; the axis represent the three analyses and labels indicate the group number and name, as well as characters governing the main split according to PCC analyses. The numbers of the Ecomorphotypes are also indicated

Missing Ecomorphotypes

Considering the matrix in Figure 5.2.2.14 the question arises: "Why are there empty spaces?" One answer is that only a subset of species was included in the analysis, missing the species that would fill the gaps; this seems too simplistic, though.

In the three dimensional space in Figure 5.2.2.14 many gaps are apparent. In fact, of the 504 possible ecomorphotypes only 20 are represented. There is considerable redundancy in the combination of the self-preservation and locomotion functional areas – as we established previously, only three ecomorphotypes are distinguished singly based on their self-preservation ecomorphotype. This is due to the inclusion of locomotion characters, and due to the oversight of important characters in the self-preservation analysis. Thus, we only discuss the 55 gaps in the 2-dimensional matrix of the 17 ecomorphotypes as defined by locomotion and feeding analyses (Table 5.2.2.1).

Table 5.2.2.1 Matrix of ecomorphotypes defined by the locomotion an feeding analyses only

		Feeding Ecomorphotype							
Locomotion Ecomorphotype		Pelagic/ demersal ram/suction feeder	Ram feeder (shark)	Ram feeder (eel)	Infaunal feeder/crusher	Crusher/biter	Benthic infaunal feeder/crusher	prober	biter
	Undulatory swimmer		1				2		
	Undulatory slow swimmer						3		
	Undulatory/ burst swimmer				4				
	Burst swimmer	5 & 6			7 & 8	9			
	Oscillatory manoeuvrer (caudal)					10			11
	Anguilliform swimmer			12					
	Oscillatory manoeuvrer (pectoral)	13 & 14			15			16	17
	Cruiser (caudal)	18							
	Cruiser (anguilliform		19				20		

The distribution of the empty fields shows that the anguilliform swimmers and the probers are both only represented by one feeding/locomotion type respectively. In the case of the anguilliform swimmer our study only included one species (*Gymnothorax parsinus*) belonging to this group. Throughout the analyses, this species separated out from the other groups. Its body shape, head form and lack of appendages distinguishing it clearly from all the other species studied. Still, it is feasible, if other anguilliformes had been included in the analyses, that they would have formed new ecomorphotypes by being anguilliform swimmers of another feeding type; thus supporting the simplistic answer given above.

The probers seem to have a feeding strategy that relies on exact manoeuvring and positioning of the body in relation to the food source. This supports the argument that any locomotion type, apart from the oscillatory manoeuvrer, is unsuitable for this feeding type. Hence, it is possible to find a oscillatory swimmer (caudal) in the prober feeding type – if the species range was sufficiently increased, but it is not expected to find any of the other gaps filled.

To explain the absence of all cruisers and undulatory swimmers from the biter and the biter/crusher rows it may again be argued that, to bite off particles of a larger prey, precise vertical manoeuvring of the body is required. This accounts for the combination of the oscillatory manoeuvrers (pectoral and caudal) with the biter feeding type but it does not explain the absence of pectoral manoeuvrers from the crusher/biter group, nor the presence of a burst swimmer in this group. The gap mentioned is very likely due to sampling limitations, similar to the ones discussed with the eel. The presence of a burst swimmer type in a feeding group requiring exact manoeuvring on the other hand warrants closer examination. This ecomorphotype has only one member: *Brachionichthys sp.2*, the Australian Handfish. As mentioned in the locomotion and feeding sections, this species was not well defined in these analyses. Although it is classed as a burst swimmer, it appears to use this locomotion mode only in an escape response, otherwise walking on its hand-like pectorals. Furthermore, it grouped with the crusher/biter ecomorphotype based on its gut structure, although observations suggest that it is an ambush predator, gulping whole prey (Green, CSIRO pers. comment).

Many of the other gaps may be explained by the strong elasmobranch/bony fish split observed in the cluster analyses. Elasmobranchs only exhibit two locomotion types: anguilliform cruisers, a locomotion style particular to sharks (*sensu* Webb 1984; Helfman *et al.* 1997), and undulatory swimmers (including the coffin ray that formed its own locomotion type). The rather limited body design of the cartilaginous fishes distinguishes them from other fish. For example, precise, small-scale manoeuvres like hovering are impossible to achieve with rather rigid, non-collapsible fins. Elasmobranchs also form their own feeding types. Their rather simple jaw structure does not allow for the diverse prey manipulations achieved by bony fish. Nevertheless, similar feeding types, with exception of biters, probers and suction feeders, are apparent. While the prior two feeding types rely, as established, on manoeuver control that are beyond the locomotion types of elasmobranches, suction feeding relies on the rapid expansion of the mouth and branchial cavity to create the influx of water – elasmobranches do not have the jaw articulation, or gill design to allow for this.

The remaining, unexplained 5 gaps are: the lack of undulatory/burst and oscillatory (caudal) swimmers from the pelagic/demersal suction/ram feeding types, the lack of caudal cruisers and oscillatory manoeuvrers (caudal) from the infaunal feeder/crusher group, and the previously mentioned absence of a oscillatory manoeuvrer (pectoral) in the biter/crusher group. The locomotion type of oscillatory manoeuvrer (caudal) appears to be a speciality of the heavily

armoured and rather plump tetraodontiformes. Suction and/or ram feeding methods need either a flexible jaw and operculum for the enlargement of the buccal cavity or a large gape, neither of which is present in these fish. The opercula of tetraodontiformes are either encased into the bony armour or reduced to a small soft slit; furthermore, their jaw is encased in the structure of the head, reducing its mobility and the size of the gape. The absence of infaunal feeders/crushers from this locomotion ecomorphotype may be due to our species selection. The same may be said for the remaining three gaps.

While some of the gaps seen in the ecomorphotype matrix really appear to be due to our limited species range, we also identified some clearly impractical, or virtually impossible combinations of feeding and locomotion types.

5.2.3 Data-set reduction for a rapid assessment approach

The recovery of the final ecomorphotypes based on a reduced character set was tested by reanalysing the data. Character set reduction was attempted in two fundamentally different ways: (a) by choosing the characters that distinguish between each of the three functional ecomorphotypes, based on the GSTA results of the three functional area analyses; (b) by recalculating an overall GSTA for the final ecomorphotypes based on the initial 'shotgun' character set.

Character set reduction (a)

Three reduced character sets based on the GSTA results of each individual functional ecomorphotype analysis were tested. The 10 or 15 highest ranking characters of each analysis, or all characters with a Kruskal-Wallis (K-W) or χ^2 value >70 in any of the analyses were used (Table 5.2.3.1). If necessary, characters were weighted according to their frequency of occurrence

Table 5.2.3.1 Subset of the GSTA results of the three separate functional area analyses, that was used for data-set reduction (showing the 10 highest ranking characters as well as all characters with a K-W/χ^2 value >70 for each analysis)

Locomotion		Feeding		Self-Preservation	
Character	**K-W, χ^2 value**	**Character**	**K-W, χ^2 value**	**Character**	**K-W, χ^2 value**
Pc_col	113	tub_snt'	112	bod_wdth	79.714
c_col	105.04	Pha_tth	93.967	pc_ar	73.416
BCI	93.074	Mth_tth	76.697	pc_b	71.895
Bod_wdth	92.657	rel_CL	73.279	bod_dpth	71.024
Pv_col	92.07	gap_ar	72.715	BCI	66.844
a_col	86.486	gillslit	72.648	ped_dpth	61.964
Ped_dpth	81.516	up_jaw_l	71.216	eye_sup	58.52363
snt_dsp	80.181	gap_wdth	67.509	pc_pos	56.676
pc_b	79.186	mth_pos	66.112	dsp_b	55.394
a_ar	77.585	gut_l	64.716	eye_diam	54.29
snt_pv	77.348	rak_flex	63.961	dsp_ar	53.007
bod_dpth	76.99	opercle	63.153	pv_ar	51.503
dsp_col	76.498	eye_diam	61.266	pv_wdth	50.592
a_b	76.417	gap_hgth	60.576	snt_dsp	49.762

Locomotion		Feeding		Self-Preservation	
Character	K-W, χ^2 value	Character	K-W, χ^2 value	Character	K-W, χ^2 value
pc_pos	75.489	pha_pyl	58.424	abdom	48.187
pv_rig	70.944	lip_uj	56.807	scl_form	46.517
a_rig	70.123	Max_ext	55.504	dsp_rig	46.036
keel	68.87	HCI	54.982	mfl	42.963
snt_dso	66.113	h_dpth	54.953	eye_pos	41.861
snt_a	64.142	lip_lj	53.896	BSP_P	40.94074
pv_b	62.141	pmax_ptr	52.935	scl_sz	38.962
sb_vol	60.861	pyl_caec	48.822	ped_SHP	36.232
scl_form	60.226	tng_dev	46.002	hsp_no	35.314
pv_ar	60.047	BSP_P	43.01269	dso_b	35.188

The success rate of ecomorphotype recovery using the GSTA of each functional type analysis was disappointing. While the phylogenetically distinct ecomorphotypes (sharks, rays, Platycephalidae, Zeidae, Macroramphosidae, Aracanidae and the Diodontidae and Tetraodontidae) were almost always recovered, the mixed groups were consistently split up or even regrouped amongst each other. Furthermore, it was interesting to observe that increasing the number of characters did not always result in better group recovery.

Character set reduction (b)

Only one character-set for ecomorphotypes based on the second reduction approach – the 30 highest ranking characters in a GST analysis of ecomorphotype groups against the entire character-set – was tested (Table 5.2.3.2).

Table 5.2.3.2 Subset of the GSTA results of the 20 ecomorphotypes analysed against all characters, that was used for the data-set reduction, showing the 30 highest ranking characters

20 Ecomorphotypes	
Character	K-W, χ^2 value
pc_loco	113
c_col	112
pc_col	112
Pha_tth	107.65
pc_b	102.19
dsp_col	97.186
BCI	96.25
HCI	95.884
bod_dpth	94.118
bod_wdth	93.873
dsp_b	90.543
pv_col	89.373
gap_wdth	88.954
h_dpth	87.969
ped_dpth	86.73
rel_CL	86.496
pc_pos	86.302

20 Ecomorphotypes Character	K-W, χ^2 value
h_wdth	86.131
pc_ar	86.121
PCI	84.359
Mth_tth	83.922
gillslit	83.446
up_jaw_l	82.007
gap_ar	81.814
a_col'	81.757
gap_hgth	81.729
pec_ang	80.131
eye_diam	79.66
mth_pos	79.402
pmax_ptr	79.171

This second approach proved more successful. Analysing a data set composed of the thirty highest ranking characters (including their respective primary characters) derived from the GSTA of the 20 ecomorphotypes, did recover them (Figure 5.2.3.1). The species separated into their pre-assigned ecomorphotypes at a dissimilarity level of 0.34, with the main exception of groups 13 and 15. Four members of the group 13 (*Apogonops anomalus*, all Scorpinidae and *Emmelichthys nitidus nitidus*) grouped with the bulk of group 6, while the non-labrid fish of the latter joined group 13. Other, minor changes included *Satyrichthys lingi* and *Sillago flindersi* switching between groups 6 and 8, inclusion of the single species group 9 (*Brachionichthys sp.2*) in group 6, inclusion of single species group 3 (*Macruronus novaezelandiae*) as an outlier of the Labridae group, and the splitting off of the Pristiophoridae from the shark group (19).

Further data reduction by eliminating characters that show high Pearsons correlation values (r^2 >0.7) resulted in the loss of the ecomorphotype groups.

Discussion

The most successful data reduction process resulted in some regrouping of the 20 ecomorphotypes, the switch of the non-labrid component of group 15 to group 13 being the most distinct. Groups 13 and 15 differ only in feeding types, the former being pelagic/demersal suction/ram feeders, the latter benthic infaunal feeders/crushers. *Latris lineata* and *Pagrus auratus*, were previously mentioned as outliers of their feeding group, being the only piscivores (Section 5.2.2), accounting for their regrouping here. The Cheilodactylidae on the other hand present a less clear cut case, however, it appears that the locomotion characters weigh more strongly in this family, than their feeding specialisation. Similarly to *L. lineata* and *P. auratus*, the Pristiophoridae formed an outlier to the shark group in the feeding analysis – their diet being mainly composed of infaunal invertebrates, in comparison to the fish and cephalopod dominated diet of other sharks. Hence, their forming a separate group is not surprising, in fact it is rather desirable. The regrouping of 5 group 13 – oscillatory swimmers – members (*A. anomalus*, *E. nitidus nitidus* and the Scorpinidae) to group 6 – burst swimmers – may be explained by the less rhomboid body shape of these species in comparison to the other members of group 13. Finally, the inclusion of various single species groups in other groupings cannot be avoided, as the reduction of the character set necessarily leads to some loss of detail.

Data reduction by retention of the ecomorphotype groups identified by three separate analyses was achieved using the thirty highest ranking characters (Kruskal-Wallis or χ^2 value >79.171) in a GSTA of the groups using all characters. The overall data-set of 63 measurements and 139 coded characters was reduced to 21 measurements (two additional measurements are needed for standardisation of the data, namely: standard length (total length for sharks) and head length) and 18 coded characters (caeca count additional, for the calculation of the relative caecum length), 6 of which are hierarchical primary characters (Appendix 5). Although the collection of 39 characters per fish does not appear like a rapid assessment method, only relatively few measurements are needed, many of which, like fin collapsibility and teeth types, are very quickly as well as easily obtained. Also, only low-skill dissection – the removal of the gut with the pyloric caeca intact – is required. Furthermore, the ecomorphotypes can be determined measuring only one adult fish per species, facilitating the sampling and speeding up the processing considerably.

It can therefore be concluded, that a rapid allocation of fish into ecomorphotypes is possible, at least in the SEF fishery.

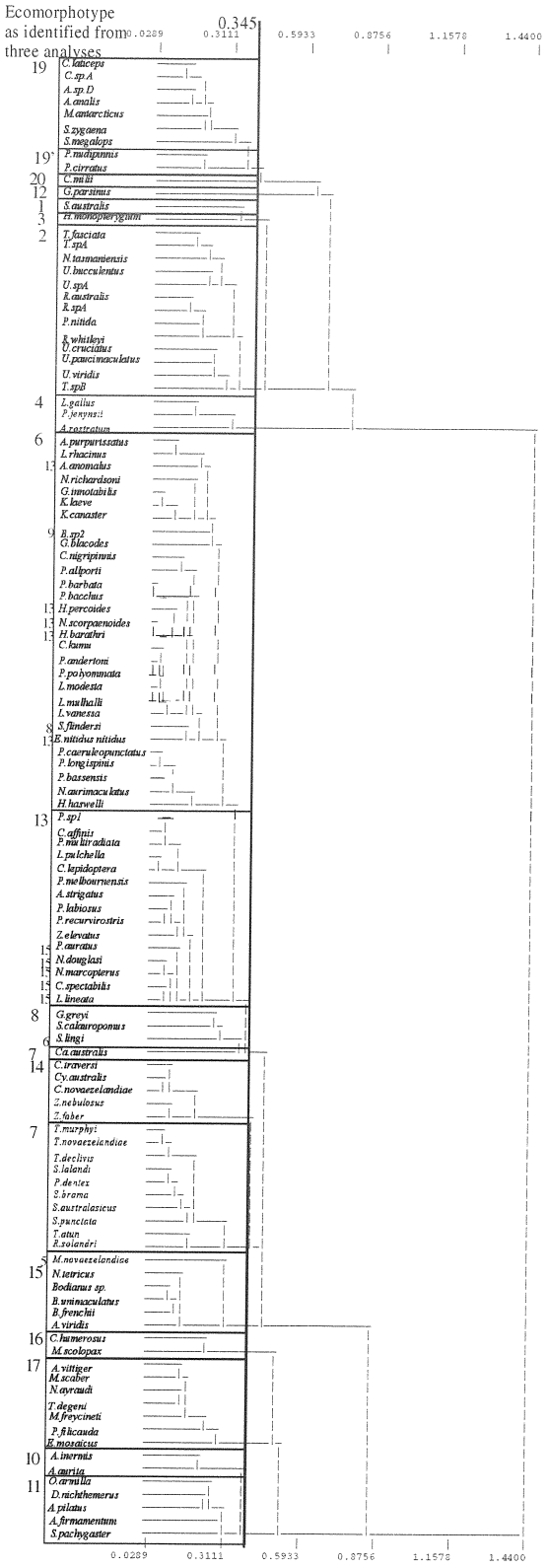


Figure 5.2.3.1 Agglomerative cluster analysis of the dissimilarity matrix of 114 species, based on a reduced character-set, using the 30 highest ranking characters (and related primary characters) in a GSTA of the 20 ecomorphotype groups on all characters (21 measurements, 18 coded characters); boxes and numbers show the recovered ecomorphotypes; small numbers indicate the ecomorphotypes of re-grouped species

5.3 Ecomorphotypes interpreted based on SEFEHS data

To assess whether the 20 ecomorphotype groups (Plate 6) correlate with ecosystem properties we assessed their compositions against data from a study of on the southeastern continental shelf region (FRDC report 94/040). Group composition was assessed in relation to habitat-association by using their relative abundances in conjunction with patterns of spatial distribution. Group composition was also assessed in relation to diet by comparing ecomorphotypes to feeding guilds established from separate analyses of stomach contents and isotopic data.

5.3.1 Habitat (seabed and water column)

Habitat association of ecomorphotypes was examined in analyses that corresponded to two levels of complexity and spatial coverage.

First, samples (fish catches from the SEFEHS study) were simply aggregated according to seabed type into 'sediment' or 'reef' habitats that had been delineated using acoustics (Bax and Williams 1999). Relative abundances of species were used to provide a classification of 'strength of association' with bottom type.

We used only samples taken with gillnet and trap because these gears were able to fish on all seabed types. Abundances were normalised for the numbers of samples from each bottom type and three categories of habitat association were recognised. Distinct association with one or other habitat (> 70% of individuals caught in habitat by both gears), and association with both (30-70% individuals caught in habitat by both gears). The degree of confidence with which species were allocated to a category was based on the source of information. High confidence: data on the species was available from the SEFEHS study; medium confidence: explicit literature references to the habitat preference of the species were found (princiupal references used: Last *et al.* 1983, Gomon *et al.* 1994 and Last and Stevens 1994); low confidence: only implicit references to the species' habitat preferences were found.

The occurrence of ecomorphotypes in the three categories was then assessed by comparing the distributions of their component species.

Second, samples were aggregated according to fish community structure, where communities were described using 1) trawl samples from a broader-scale survey of sediment habitats, and 2) the gillnet samples from the previous analysis. Community types were delineated from multivariate analysis of fish biomass data (FRDC report 94/040), and the proportions of ecomorphotypes in each community type assessed using absolute biomass and numbers separately.

Seabed habitat association

Sediment flats are the preferred habitat of the majority of the ecomorphotypes when abundance is taken into account. Eight types (1, 2, 4, 5, 8, 14, 16 and 20) are strongly associated with sediment habitats, seven (6, 10, 11, 13, 17, 18 and 19) use both habitats but are considerably

more abundant on sediments than reef, and only two ecomorphotypes (12 and 15) were more abundant on reefs or strongly reef-associated (Figure 5.3.1.1). Ecomorphotype groups 3, 7 and 9 were not caught by gillnet or traps and there is no indication of their seabed habitat association in the literature.

Ecomorphotypes strongly associated with sediment habitats have a variety of feeding modes being infaunal feeders/crushers with inferior or downwards protruding mouths (groups 2, 4, 8 and 20), probers with tubular snouts (group 16), or ram/suction feeders, some with protrusible jaws (groups 1, 5 and 14). Most are strongly compressed, either dorso-ventrally (groups 1, 2, 4) or laterally (groups 14 and 16). (In our data, the 'blind side' of pleuronectiformes corresponds to the ventral surface of other fishes.)

Three contrasting patterns can therefore be seen among ecomorphotypes adapted to living in temperate shelf sediment habitats. The first is strong dorso-ventral compression with weak undulatory swimming, dull colouration for camouflage on or in sediments, and an infaunal feeding mode (rays, pleuronectiformes: groups 2 and 4) or ambush prey capture (*Squatina australis:* group 1). Second is strong lateral compression with relatively weak oscillatory swimming, reflective colouration for camouflage in the water column, and a feeding mode involving prey capture over the substrate, probably often high in the water column (Zeidae, Macroramphosidae- predominantly *M. scolopax* on the shelf: groups 14 and 16). Species comprising the third pattern (*Synchiropus calaruopomus*, *Gonorynchus greyi*, *Sillago flindersi*: group 8) are only moderately compressed and variously coloured, but have in common an elongate form, small body size, a diet based predominantly on infauna, with burst-speed capability for greater mobility and predator avoidance over substrates. Group 5 (*Macruronus novaezelandiae*) is unlike the remainder of strongly sediment-associated ecomorphotypes but is represented on the shelf only by the juvenile life-history stage during its cross-shelf ontogenetic migration to upper-slope depths. Another single-species, *C. milii,* (group 20) shares some morphological features with other patterns but remains something of an outlier.

Ecomorphotypes that are abundant on sediments but with a degree of reef-habitat association are made up by two groups with distinctive patterns, and two groups consisting of several species. A mix of benthopelagic families and sharks (groups 18 and 19) are distinctive in being 'cruising', ram/suction feeders, and the Tetraodontiformes (groups 10, 11 and 17) in being weak oscillatory-swimming, crushers/biter or biters. The two relatively undifferentiated groups are 'generalist' ram/suction feeders with either burst swimming mode (groups 6) or oscillatory swimming mode (group 13).

Benthopelagic 'cruising' ram/suction feeders (Carangidae, Gempylidae, Scombridae, Centrolophidae: group 18) are relatively large-bodied, fusiform fish with a strongly forked tail and narrowly necked, often keeled caudal peduncle designed for sustained, fast swimming, and extensive use of the watercolumn. Long, bristly gillrakers, in conjunction with the large gape and large gill slit opening, enables sieving of small pelagic prey, or capture of larger gelatinous zooplankton. Sharks (group 19) are similarly large-bodied, fusiform and designed for extended periods of cruising, although they have been reported to preserve energy by resting on the sediments (Webb 1984). They employ anguilliform movement to achieve this swimming mode, capitalising on the strategic placement of their rigid dorsal and anal fins and on their heterocercal tail (*sensu* Helfman *et al.* 1997). Sharks have an inferiorly positioned mouth; they employ ram feeding techniques, but rely more on an ambush style attack. While this group

prefers the sediment flats, its members are highly mobile predators of fish and cephalopods leading them to venture between habitats.

At first glance, the association of three slow manoeuvrers, crusher/biter and biter, type 10 (Diodontidae and Tetraodontidae), type 11 (Aracanidae) and type 17 (Monacanthidae) with sediment flats, as well as reef habitats, is surprising. However, all three types have distinctive self-defense mechanisms that deter potential predators, giving them the freedom of exploiting more open areas that are too dangerous for more vulnerable ecomorphotypes. Ecomorphotypes 10 and 11 have a highly spherical body shape (inflatable in the prior, bony, rigid in the latter) and rely on oscillatory swimming, using the propulsive force of their fleshy, rounded caudal peduncle. These fish also have a highly developed swim bladder allowing for precise buoyancy control. The former are crusher/biters feeding on molluscs and hermit crabs, hence even specialising on prey found in the open sediment flats, the latter are biters feeding on colonial organisms, accounting for their association with the reef-habitats. The Monacanthidae are also biters; their body is discoid, laterally flattened with a rigid, interlockable dorsal spine further increasing the body depth. They rely on a slow oscillatory swimming style, augmented by undulatory use of their second dorsal fin (Lighthill and Blake 1990).

Our overall analysis did not provide differentiation of the two generalist ecomorphotypes (groups 6 and 13) but their component species showed some clear within-group divergence of habitat use. Members of ecomorphotype 6, deep-tailed, burst-swimming, large-mouthed ram feeders were distributed across the habitat preference categories, but there was a distinct trend of preference for sediment flats by fishes with a large pelvic body width – i.e. a broad ventral surface (e.g. Platycephalidae and Triglidae), as opposed to the reef preference of the laterally compressed species (e.g. Moridae). Ecomorphotype 13 differs from type 6, by being in general more reef-habitat associated with only a small proportion (<20%) showing strong association to sediment flats. The type 13 fishes are similarly to type 6 ram/suction feeders, but they tend towards a more discoid shape (moderate degree of lateral compression – similar to type 15) and are slow oscillatory swimmers using their large pectorals in an oar-like fashion (Webb 1984) for precise manoeuvring in structured habitat. The more elongate species of this ecomorphotype appear to move freely between the habitats, while the more clearly discoid fish associate closer with the reef-habitat.

The two reef-associated ecomorphotypes are infaunal/epifaunal feeders/crushers with well-developed dentition and lips for feeding on hard-bodied prey (group 15), and the piscivorous single anguilliform eel *Gymnothorax prasinus* (group 12). Again, two contrasting ecomorphological patterns can be seen as adaptations to living in temperate shelf reef habitats. Group 15 fishes (Labridae, Cheilodactylidae, Latridae and Sparidae) are mostly large-bodied, with a discoid body shape (a moderate degree of lateral compression), well-developed pectoral fins for controlled manoeuvring in structured habitat, and strong colour patterning for camouflage against hard-substrate with relief and attached epifauna. The primary feature of the eel's form, a greatly elongated body, is an adaptation for crevice dwelling.

Are ecomorphotypes still valid when their component species are examined with respect to habitat association in the same way? Among ecomorphotypes containing more than one species, several remained unaltered (Plate 7). These were mainly the 'strongly-associated' groups (2, 4, 8, 14, 16), although the Cheilodactylidae (*Nemadactylus macropterus* and *N. douglasii*) from the reef-associated group 15 were seen to also have a sediment-association. There was divergence among species from the 'reef and sediment-associated' ecomorphotypes,

particularly the large mixed groups (6 and 13), with strong associations shown by several species for one or other habitat type. Most of group 6, relatively small and elongate or dorso-ventrally flattened fishes with large pelvic body width (i.e. broad ventral surface) and long-based, sub-central/deep pectoral fins (Triglidae, Chlorophthalmidae and Platycephalidae, Uranoscopidae), showed a strong sediment association. Whereas several discoid, moderately lateral compressed, group 13 fishes with short-based sub-central pectoral fins (Serranidae and Pempheridae) are reef-associated. These patterns are generally consistent with those seen in the strongly-associated ecomorphotype groups that remained unaltered.

These changes indicate levels of sub-structure in ecomorphotypes that are not surprising given the large number of species (114) with wide morphological diversity targeted by our 'shot-gun' approach. The changes also indicate the opportunities that exist to refine the analytical strategy. Refinements would include examining large generalist groups in analyses that are independent of 'extreme' morphotypes, e.g. those that form single-species ecomorphotypes and therefore reduce the contrast of more-similar morphotypes.

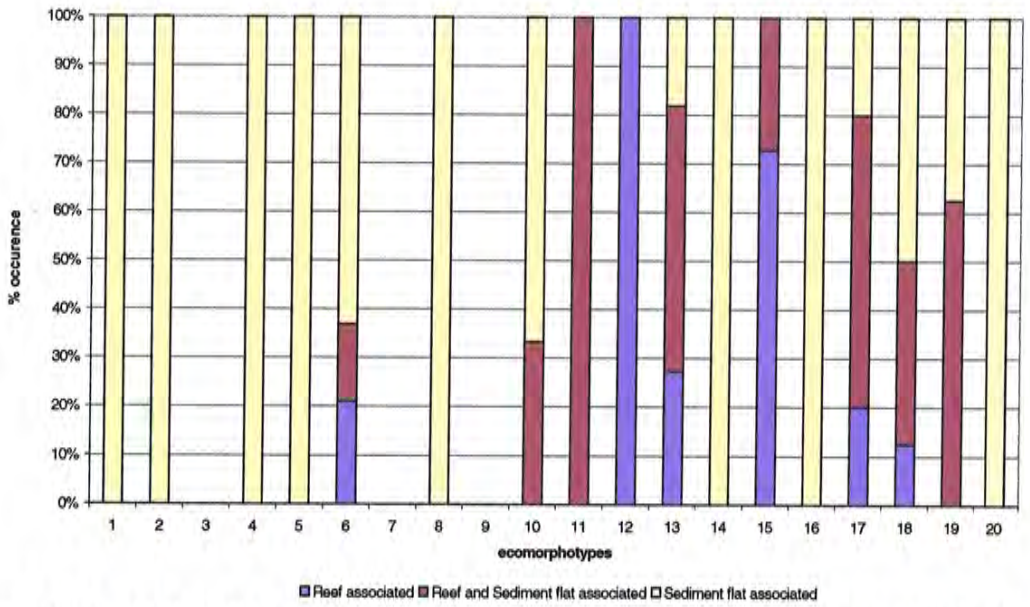


Figure 5.3.1.1 Distribution of habitat association of species (reef/sediment associated: >70% occurrence in the respective habitat, reef and sediment flat associated: 30-70% occurrence in either habitat) in the 20 ecomorphotypes identified in the present study, displayed as % occurrence in each ecomorphotype

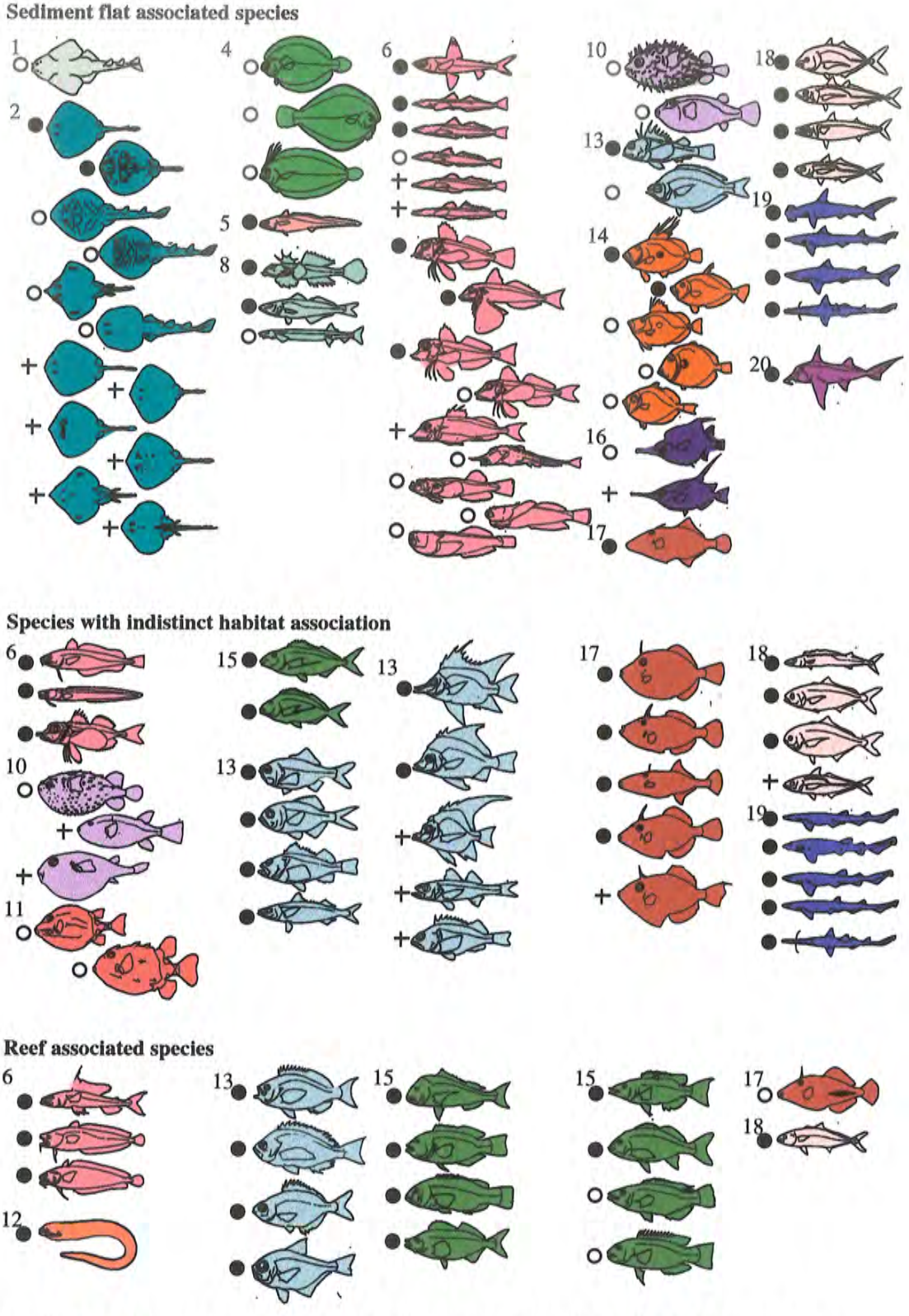


Plate 7 Habitat association of species (reef/sediment associated: >70% occurrence in the respective habitat, indistinct association:30-70% occurrence in either habitat) in the 20 ecomorphotypes (indicated by colour and numbers)
Confidence levels: ● high confidence (data from SEFEHS), ○ medium confidence (explicit literature reference to habitat), + low confidence (implicit literature references to habitat)

Relationships between ecomorphotype and communities

Sediment communities

Fish communities on sediments of the southeastern shelf region (identified from analysis of biomass in trawls) are structured primarily by depth (inner, mid and outer shelf) and location (north-south distribution) (FRDC report 94/040). There are three inner shelf community regions- southwest (ISW), central (IC) and northeast (INE)- and two regions each on the mid- and outer shelf: mid-southwest/central (MSWC), mid-northeast (MNE), outer-southwest/central (OSWC), and outer- northwest/central (ONWC).

Overall, fish communities on sediments are dominated in biomass by ecomorphotypes with mixed (sediment and reef) associations: predominantly benthopelagic cruisers (type 18) and generalist ram/suction feeding, oscillatory swimmers (type 13) (Figure 5.3.1.2). Benthopelagic cruisers consistently comprise ~20-30% of biomass in each community, but make up ~60% at ISW due to high abundance of the single most important group 18 species, *Trachurus declivis* (Carangidae)- a fusiform fish of moderate size with a deeply forked caudal fin, strongly keeled, narrowly necked peduncle, and median as well as lateral fins that collapse into groves increasing its streamlining. In contrast, the second major group – generalist ram/suction feeding, oscillatory swimmers – comprise considerably greater biomass in communities of the outer shelf and the MNE compared to those of the inner shelf and the MSWC (~40-50% c.f. ~5-8%). They account for much of the similarity of the MNE and outer shelf communities, and the dissimilarity between the two mid-shelf communities. Generalist ram/suction feeding, burst swimmers (type 6) were present in all communities but distinctly most abundant (~20%) in the MSWC. Interestingly, ecomorphotypes with strong-sediment association (types 1, 2, 4, 14, 16 and 18) comprise a relatively small fraction of biomass in sediment communities – although rays (type 2) are moderately abundant on the inner-shelf, particularly at IC.

Community compositions analysed by numerical abundance emphasised the ecomorphotypes containing relatively small-bodied fishes and de-emphasised those containing large-bodied fishes. The overall dominance of pelagic cruisers (type 18) and generalist ram/suction feeding, oscillatory swimmers (type 13) were similar to patterns in biomass compositions (Figure 5.3.1.3). Also, generalist ram/suction feeding, burst swimmers (type 6) were present in all communities and distinctly most abundant in the MSWC. However, there were several notable differences. Generalist ram/suction feeding, oscillatory swimmers made up higher proportions in every community, and on the outer shelf they contributed > 80% numbers due primarily to *Apogonops anomolous*. Benthopelagic cruisers made up a greater proportion in IC, but otherwise distinctly decreased in importance with distance offshore. Rays (type 2) showed the same trend in proportions across communities but were de-emphasised. Two strongly sediment-associated ecomorphotypes (8 and 16) were more prominent. The moderately compressed, small, elongate, burst-speed swimming, infaunal feeders in inner shelf communities – due to *Synchiropus calaruopomus* and *Sillago flindersi,* and the laterally-compressed, weak oscillatory swimming, benthopelagic probers on the mid-shelf (especially MNE) – due to *Macroramphosus scolopax.*

The greater degree of dominance in the analysis of numerical abundance compared to biomass (particularly by type 13) had the overall effect of de-emphasising the diversity (richness) of ecomorphotypes. Diversity was generally higher on the inner shelf (a maximum of 13 groups at INE) and lower on the outer shelf (Figures 5.3.1.2 and 5.3.1.3).

How do patterns in ecomorphotype composition compare to those in communities based on multivariate analysis of (double square-root transformed) biomass? Depth-related patterns were evident in both structures but locational (north-south) patterns were less distinct among ecomorphotypes: three distinct inner shelf communities had a broadly similar ecomorphotype composition, as did the two outer shelf communities. However, a distinct difference was apparent between the two mid-shelf ecomorphotype compositions: MSWC is more diverse and resembles the inner shelf, whereas MNE resembles the outer shelf (in biomass) due to the dominance of ecomorphotypes 13 and 18 (Scorpaenidae, Serranidae, etc. – discoid, oscillatory swimmers (pectoral), ram/suction feeders and Carangidae, Centrolophidae, etc. – torpedo-shaped, cruisers, ram/suction feeders) and is strongly influenced (in numbers) by the laterally-compressed, weak oscillatory swimming, benthopelagic prober *Macroramphosus scolopax* that is relatively scarce inshore and southwards. The MSWC forms the middle of the very wide, slowly dropping shelf off the southeastern corner of mainland Australia, while the MNE represents a very narrow midshelf, sharply dropping off towards the outer shelf and the shelf edge. Thus, the ecomorphotype distribution reflects the relative proximity of the MNE and the MSWC to the shallow inner shelf and to the outer shelf/shelf edge, respectively.

Ecomorphotypes allow us to see broader, more functionally based patterns of the shelf community that may be masked by regional differences in species composition.

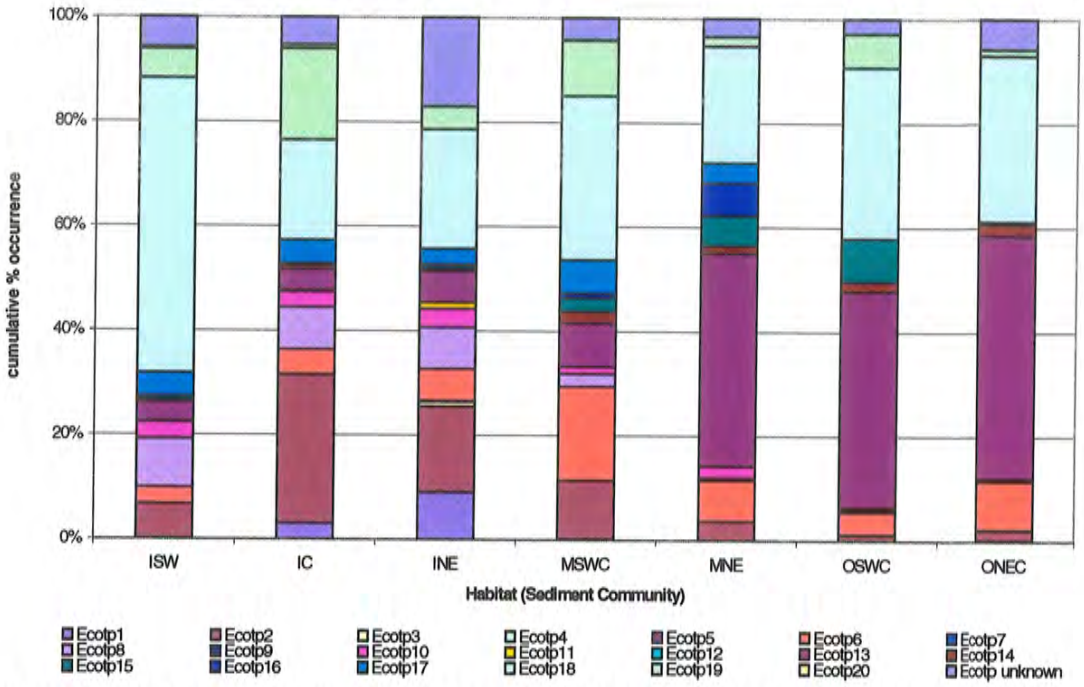


Figure 5.3.1.2 Distribution of ecomorphotypes in sediment habitats of the southeastern shelf region (identified from analysis of biomass in trawls) represented as % occurrence by biomass

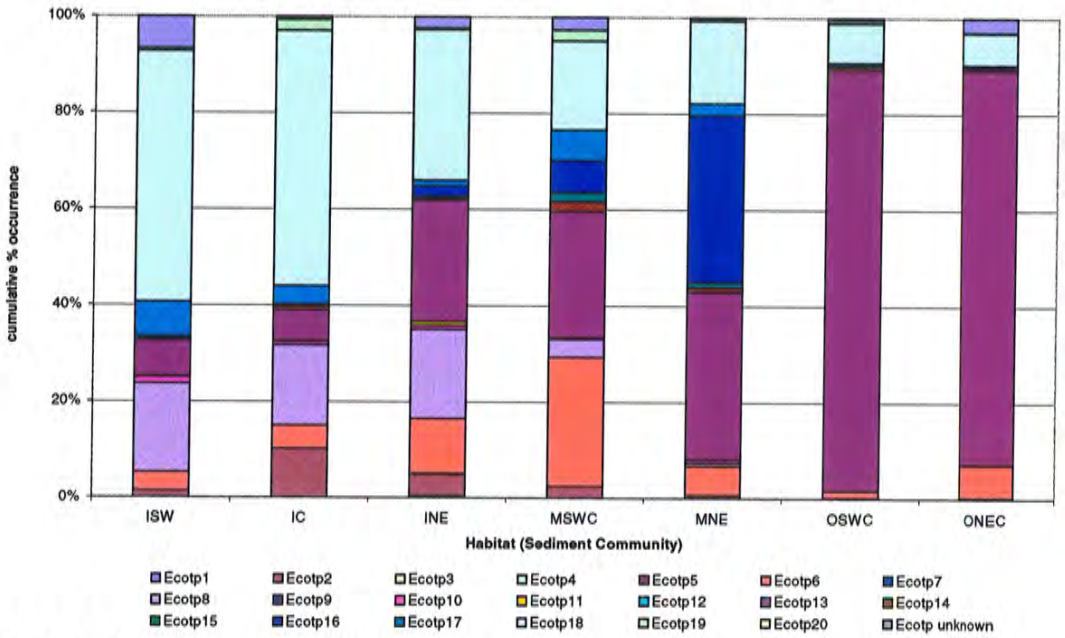


Figure 5.3.1.3 Distribution of ecomorphotypes in sediment habitats of the southeastern shelf region (identified from analysis of biomass in trawls) represented as % occurrence by numbers

Reef communities

Fish communities on reefs and adjacent sediments of the southeastern shelf region (identified from analysis of biomass in gillnets) are structured primarily by seabed type, depth (inner, mid and outer shelf) and location (north-south distribution) (FRDC report 94/040). There are four inner shelf community regions- inner reef (IR), inner sediments (IS), reef off Point Hicks (PHR) and adjacent sediments (PHGI); the latter site corresponds closely to the IC community region identified from trawl catches. In addition, there are two community regions the outer shelf – outer reef (OR) and outer sediments (OS) (the latter corresponding closely to ONEC and OSWC communities identified from trawl catches) and one at the shelf-break (H).

Overall, fish communities in reef and adjacent sediments sampled by gillnet are highly dominated in biomass by ecomorphotypes with mixed (sediment and reef) associations: predominantly ram/suction feeding, demersal and benthopelagic cruisers (types 18 and 19) (Figure 5.3.1.4). Combined, they make up > 60% of all communities, with sharks (type 19), in particular *Cephaloscyllium laticeps*, characterised by their elongate body, their distinctive fin distribution and by their large inferior mouths with grasping teeth, making up nearly all biomass at the reef and sediments off Point Hicks (PHR, PHGI), and benthopelagic cruisers (mainly Carangidae and Centrolophidae characterised by torpedo-shaped body, deeply forked tail, and narrowly necked, strongly keeled peduncle) making up 60-70% of biomass in the IS and OS communities. As would be expected from patterns in habitat association, the strongly reef-associated ecomorphotype (group 15) was present in all reef habitats, but comprised a maximum of only ~20% of biomass at OR. Reef-associated species from the two generalist ecomorphotypes (6 and 13) were also present in reef communities, particularly at the shelf-break (H).

The corresponding analysis based on numerical abundance was broadly similar to the biomass analysis (Figure 5.3.1.5). However, the reef-associated ecomorphotype (15) and reef-associated species from one the two generalist ecomorphotypes (13) were slightly emphasised.

The reef community based distribution of ecomorphotypes does not show as clear a pattern as the more broad-scale sediment community. The dominant trend observed here reflects the selectivity of gillnets for certain ecomorphotypes (types 18 and 19), rather than the ecomorphotype distribution over the communities. However, the relative replacement of the teleost cruiser type (18) by the elasmobranch cruiser type (19) in the Point Hicks area (PHR, PHGI) suggests that these two ecomorphotypes are functional equivalents, even though the two taxonomic classes arrived at this corresponding functional type along different evolutionary paths.

Gear selectivity proved to be a confounding factor in this analysis. A general comparison of trawl with gillnet shows, in both biomass and numerical abundance data, that more ecomorphotypes are caught by trawl and that there is a higher degree of dominance in gillnet catches (i.e. they are more selective). Gillnet is highly selective for sharks (type 19), and to a lesser extent, benthopelagic cruisers (type 18) and the strongly reef-associated ecomorphotype (15). Trawls select for strongly sediment-associated types (2 and 8) and, to a lesser extent, the oscillatory swimmer, biter (ecomorphotype 17 – Monacanthidae). This observation forms the foundation for another interesting application of ecomorphology – as an indicator for vulnerability to gears.

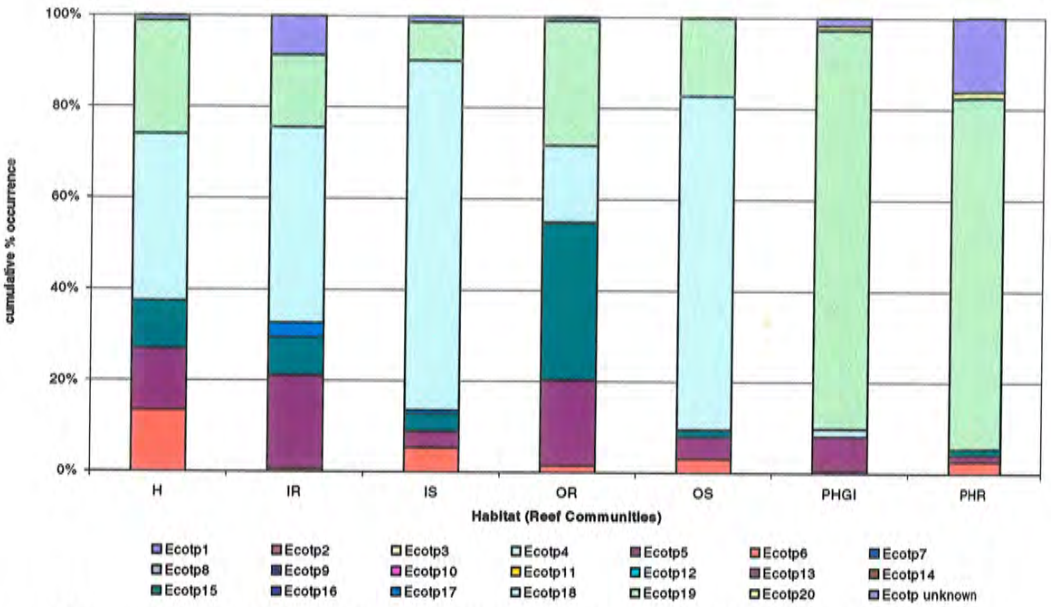


Figure 5.3.1.4 Distribution of ecomorphotypes on reefs and adjacent sediments of the southeastern shelf region (identified from analysis of biomass in gillnets) represented as % occurrence by biomass

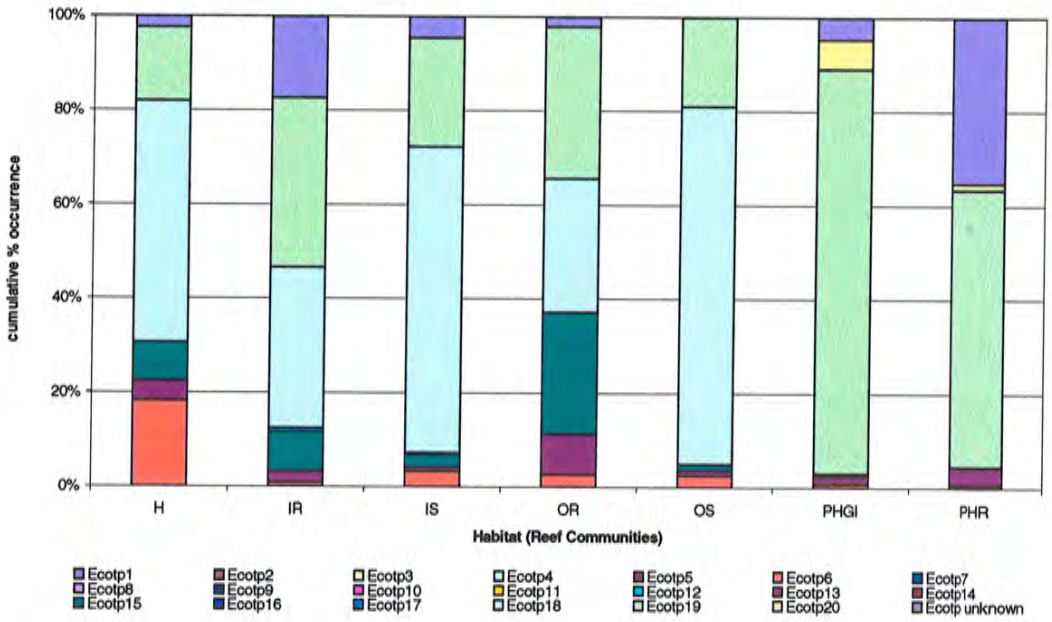


Figure 5.3.1.5 Distribution of ecomorphotypes on reefs and adjacent sediments of the southeastern shelf region (identified from analysis of biomass in gillnets) represented as % occurrence by numbers

5.3.2 Diet

In the SEFEHS, dietary data were collected at the highest level of taxonomic resolution, but analysis of a dataset containing over 500 prey taxa and 70 fish species proved prohibitive. Prey taxa were therefore first grouped taxonomically, and then by major habitat categories - benthic, bentho-pelagic and pelagic (Bax and Williams 1999). Feeding guilds were identified in a hierarchical cluster analysis.

To examine the distribution of these feeding guilds in the 20 ecomorphotypes identified here, we assigned the 51 species that overlap between the dietary study and the present project to their respective ecomorphotypes and calculated the percentage occurrence of feeding guilds in each ecomorphotype (Figure 5.3.2.1). All feeding guilds identified were represented by two or more ecomorphotypes. However, seven ecomorphotypes (3, 4, 5, 9, 11, 12 and 20) could not be assigned to a feeding guild, as there was no species overlap.

Piscivory is prevalent (>70%) in ram and some ram/suction feeders; namely in ecomorphotypes 1 (*Squatina australis*) and 19 (sharks) – ram feeders, as well as in types 6 (Platycephalidae, Triglidae, Uranospopidae, etc.), and 14 (Zeidae) – ram/suction feeders. All these types have a large gape and grasping teeth. Sharks are cruising ram feeders, pursuing benthic as well as bentho-pelagic fish, taking advantage of their fast, sustained swimming mode. The remaining piscivorous ram, ram/suction feeders are ambush predators. *S. australis* feeds exclusively on benthic fish, using movement of the enlarged pectoral fins and a burst from the muscular tail to launch from the seabed to capture prey overhead. Type 6 species do not exclusively feed on fish, but also take benthic crustacea and invertebrates. Their generally dorso-ventrally compressed body form with broad ventral surface allows these fish to ambush prey from a sedentary position on the sediment, using their muscular tail, augmented by the long-based dorsal and anal fins for short fast bursts of swimming, when they strike – a lie and wait technique (*sensu* Gerking 1994). However fish of this ecomorphotype also actively forage for benthic crusteacea. Consistent with their habitat association above sediment flats, Zeidae feed up in the watercolumn. They principally consume bentho-pelagic fish, but also feed on various pelagic prey (pelagic crustacea/omnivore guild). This ecomorphotype may be described as a stalker (*sensu* Gerking 1994). Barely visible in the watercolumn, due to their narrow body and reflective colouration, they stalk their prey using both slow oscillatory and undulatory movement of the pectoral and dorsal/anal fins, respectively (*sensu* Lighthill and Blake 1990). The strike however does not involve a swimming burst – these fish are not designed for that; Zeidae have a highly protrusible mouth, a quick extension of which may be used to bridge the last gap between fish and prey in a rapid strike(*sensu* Gerking 1994). In addition, the suction force created by this rapid extension further augments the capture of the prey.

In ecomorphotype 15, 40% of species included here are piscivores. This relative dominance of piscivores in an oscillatory manoeuvrer, infaunal feeder/crusher type with a long gut, not well-defined stomach and molariform pharyngeal dentition is surprising. However, these 40 % are made up of the two species we identified as outliers in the feeding analysis – *Pagrus auratus* and *Latris lineata*.

Benthic invertebrates as prey were subdivided into megabenthos (large crustacea and some molluscs), small crustacea, non-crustacean invertebrates and polychaetes.

The benthic invertebrate/omnivore (megabenthos) feeding guild is only dominant (>60%) in ecomorphotype 2, the rays. These undulatory swimming, benthic infaunal feeders/crushers have small ventral mouths with strong, molariform teeth plates. As their eyes are situated dorsally, these fish have a highly developed sensory system to aid prey detection. As discussed in the previous section, these fish strongly associate with sediment flats. A smaller proportion (20%) of species of ecomorphotype 15 also belong to this feeding guild. This oscillatory swimmer, infaunal feeder/crusher type is similarly characterised by molariform tooth plates – pharyngeal teeth, though.

There is a high association of polychaete feeders with the above feeding guild in the ecomorphotypes, comprising more than 30 and exactly 20% of species belonging to ecomorphotypes 2 and 15, respectively. The characteristics of both these types are detailed in the previous paragraph. Ecomorphotype 8, a burst swimming infaunal feeder/crusher type composed of only three species also includes a polychaete feeder – *Sillago flindersi*. The only other species of this type overlapping with the dietary study (*Synchiropus calauropomus*) belongs to the benthic invertebrate (non-crustacea) feeder guild.

This latter feeding guild clearly dominates the ecomorphotypes 10 and 17 (>60 and 100% of species, respectively). Type 10, the Diodontidae and Tetraodontidae, are crusher/biters with large molariform teeth with a cutting edge, and a long indistinct gut. The diet of type 10 fish consists largely of molluscs (mainly gastropods) and some hermit crabs. Type 17, Monacanthidae, are biters. These fish have small mouths with strong, incisiform teeth and long indistinct guts to process hard, difficult to digest food like bryozoa, ascidians and sponges.

The feeding guild of 'other small benthic crustacea' contains *Macroramphosus scolopax* the only prober, oscillatory manoeuvrer in the dietary study, and *Caelorinchus australis*, the continental slope species, burst swimmer, infaunal feeder/crusher ecomorphotype. The former type has a tubular snout, a highly specialised feeding apparatus for probing in crevices for small prey like isopods and amphipods or sucking such organisms out of the watercolumn. The latter has an inferior mouth with well developed lips, possibly for picking similar prey from substrates.

The term 'pelagic to bentho-pelagic omnivore' best describes ecomorphotype 18 – Carangidae, Centrolophidae, etc. bentho-pelagic piscivores (>30%) pelagic invertebrate feeders (>20%) and both pelagic and bentho-pelagic omnivores (10% each) are the feeding guilds the species of this cruising ram/suction feeder type belong to. The feeding modes of these fish may be described as either passive filtering of invertebrates while swimming through the watercolumn, making use of the sieving device of long bristly gillrakers, or pursuit piscivory, similar to the shark group.

Ecomorphotype 13 fishes – oscillatory manoeuvrer, ram/suction feeders must be termed true generalists. The species of this type belong to any feeding guild from polychaete feeder to pelagic crustacea feeder/omnivore. This ecomorphotype combines fish with various gapes, and varying degree of lateral compression. It appears that either this type is not as clear a functional unit, as other ecomorphotypes, or fishes that group in this type truly are opportunistic, filling ecological niches where they occur.

The type of food taken by different ecomorphotypes does relate to the feeding and locomotion type assigned to them. However, feeding guilds assigned to species on the basis of stomach content analysis – aggregated by taxonomy and habitat – do not necessarily reflect the ecomorphotypes. These observations again support the argument presented in the feeding type analysis, that different prey aggregation methods based on functionality, related to habitat, life style and self-preservation mode, rather than on taxonomy may result in clearer trend-definitions between ecomorphotypes and feeding guilds. However, such prey aggregation is difficult, as often less is known about the prey organisms, than of the predators.

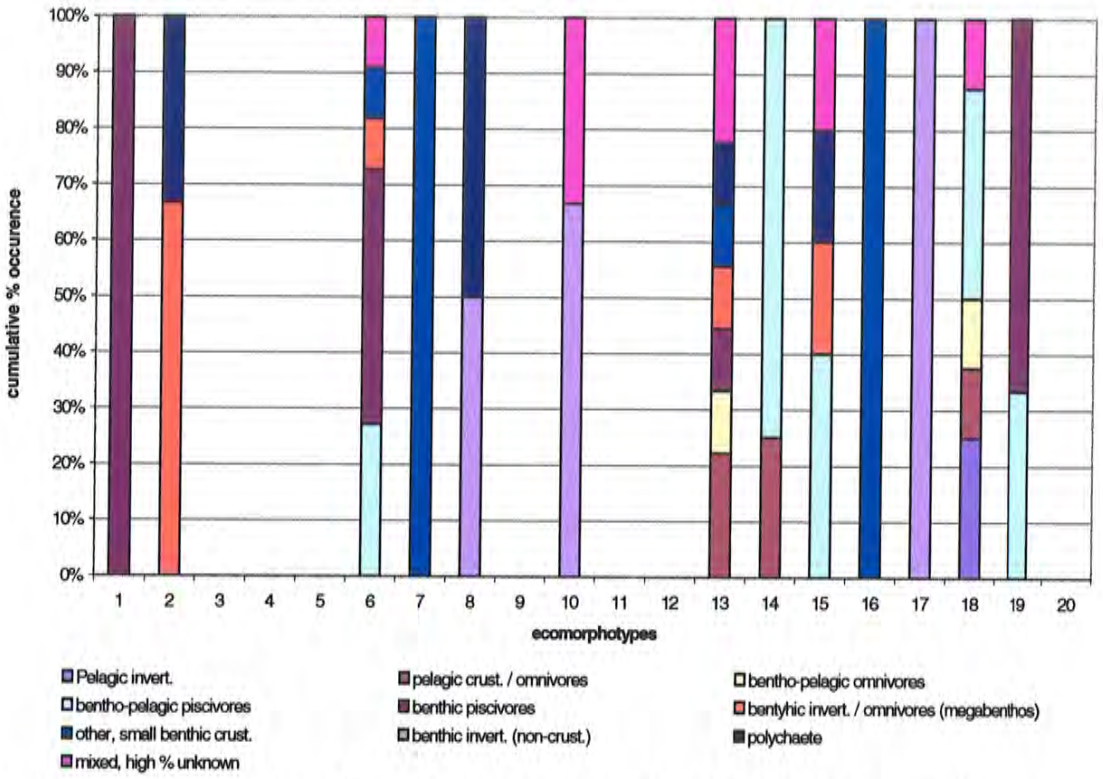


Figure 5.3.2.1 Distribution of feeding guilds (determined in the SEFEHS) in the 20 ecomorphotypes identified in the present study, displayed as % species of each guild

5.3.3 Trophic levels and stable isotopes

Stomach content data and stable isotope data give different information: while the prior indicate what the specimen has ingested recently, the latter relate to the diet assimilated over an extended period, up to several weeks from the time of tissue analysis, and as such suggests the trophic niche in which the specimen has been feeding rather than specifying the prey ingested (Bax and Williams 1999).

Stable isotope values (mean °/oo $\delta^{15}N$, $\delta^{13}C$) were available for 57 of the 114 species from the SEFEHS project. Using these values we calculated the mean $\delta^{15}N$ and $\delta^{13}C$ for each ecomorphotype group where data were available, and plotted them, ordered by increasing isotope level, with an error bar indicating the range within the group (Figure 5.3.3.1). No data was available for any member of ecomorphotypes 3, 5, 9 and 11the data show no clear trend between ecomorphotypes.

In the SEFEHS report (Bax and Williams 1999) data from the present study was used for the interpretation of the isotope values. In particular, regressions were calculated between the $\delta^{15}N$ and $\delta^{13}C$ values and the gut length, number of pyloric caeca and length of longest caecum. The only significant relationship found was a negative regression($r=-0.43$; $p=0.0008$) of $\delta^{13}C$ and gut length indicating the common finding that fish with shorter guts feed at higher trophic levels, than fish with longer guts.

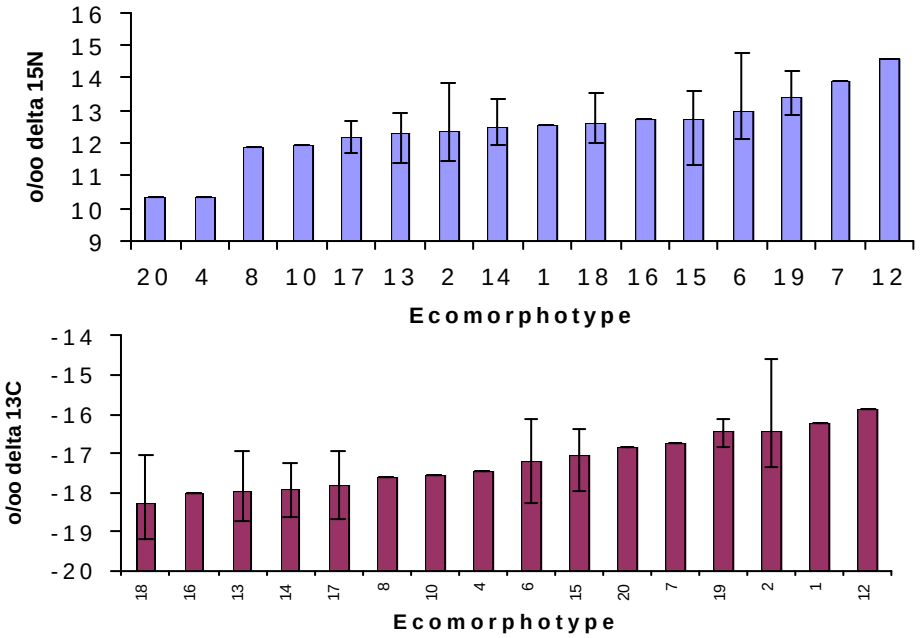


Figure 5.3.3.1 Plot of mean stable isotope ratios (°/oo $\delta^{15}N$, $\delta^{13}C$) for ecomorphotypes, including standard deviation error bars (where error bars are absent, only one sample was available)

5.4. Application of Ecomorphology

5.4.1 Understanding ecosystem interactions

Ecosystem Management and Ecologically Sustainable Development frequently appear as goals of marine natural resource managers, including AFMA. Achievement of these goals will require an understanding of ecosystem interactions so that the direct impact and flow-on effects of specific management interventions can be predicted. The complexity of marine ecosystems is such that explicit representation of all species in models is not feasible, even of fish alone. 'Representative' or 'indicator' species must be chosen, or species must be grouped and replaced by 'surrogates' (Ward *et al.* 1998). Several techniques have been used to group fish species:

- Taxonomic groups
- Size groups
- Direct trophodynamic grouping from diet (based on stomach content analysis)
- Indirect trophodynamic grouping derived from stable isotope ratios
- Species assemblages

In Section 1 we discussed the recent shift of emphasis in community management away from phylogenetic towards functional groups (Bahr 1982; Barbosa and Galdean 1997; Grime 1997). The techniques listed above tend towards functional grouping of species, particularly the two based on trophodynamics, but they do consider only one function or process at the time. Furthermore, they require extensive and expensive studies to provide the information required for grouping.

Ecomorphotypes can provide one view of a system that combines both species level and functional information (e.g. habitat use) at different levels of resolution. They provide an alternative to choosing between species or habitat as surrogates for selecting marine reserves (Ward *et al.* 1998) and provide greater information on ecological processes than either species or habitat. Furthermore, ecomorphotypes can be identified relatively rapidly and inexpensively – we recovered the basic ecomorphotypes from a dataset of 21 measurements and 18 coded characters, measuring only one fish per species.

Comparison of ecomorphology with other data-reduction techniques applied to ecosystem data

Taxonomic groups

Taxonomy at the family-level is mirrored, to a great extent, in the 20 ecomorphotypes we identified – co-familials always grouped together. However, only 4 of the 13 groups with two or more members are represented by a single family. Thus the ecomorphotypes, at the present level of detail, represent a slightly higher level of grouping than family, based on functionality.

Several studies of marine and freshwater invertebrate communities have suggested that community-level impacts can be detected with the same power at the family level as at the species level (Ferraro and Cole 1990, James *et al.* 1995, Sommerfield and Clarke 1995, Bowman and Bailey 1997). It is intriguing that a slightly higher level than the family would also seem sufficient to measure system-level changes in this marine fish community.

However, system-level changes are not the only changes of interest in the management of marine communities: some differences that could be expected to show in grouping by functionality rather than taxonomy are not manifested in the 20 ecomorphotypes. One example is the previously mentioned non-distinction of *Neoplatycephalus richardsoni,* which has a swimbladder and feeds on pelagic fish, from other Platycephalidae species that lack a swimbladder and feed on more benthic resources. However, *N. richardsoni* is not the only species with a functional swimbladder in its ecomorphotype (e.g. Triglidae and Moridae). To some extent this may reflect how fine we were prepared to make the distinctions between ecomorphotypes – how many groups we wanted to distinguish – but it may also indicate that we omitted an important functional area: use of the demersal or pelagic environments.

Size groups

Size affects interactions between fish. Large fish are less vulnerable to predation – they are too large for many predators and they can swim faster than smaller fish (*sensu* Whitehead 1975). In the present study we eliminated the size factor from all characters by using relative measurements, as we wanted to avoid masking similarities in functionality by size. However, we did include overall size (MFL), untransformed, into all analyses and it did not stand out as a defining character for any of the functional ecomorphotypes, with the exception of self-preservation group 4, which combined sharks with the Carangidae, Centrolophidae group. Considering the well-documented importance of size in fish-community structure (e.g. Mann 1988, Pope 1989, Gomes 1993, Paradis et al. 1996), we propose that a size-class factor should be overlaid onto the ecomorphotypes, if this type of grouping is used in ecosystem management or assessment.

Direct trophodynamic grouping from diet

The most common method of studying ecological processes in marine ecosystems is to analyse the diet of the fish, their predators and prey. However, as mentioned above, such studies are extensive and expensive. In the present project we identified 8 ecomorphotypes based on their feeding-related morphology, and 20 ecomorphotypes when locomotion and aspects of self-preservation are included. Although the type of food taken by different ecomorphotypes does relate to the feeding and locomotion type assigned to them, the feeding guilds assigned to species on the basis of stomach content analysis do not reflect the ecomorphotypes (Section 5.3.2).

Dietary data, even if it is collected at the highest level of taxonomic resolution, is generally first grouped taxonomically, and then by taxonomic, size or habitat categories (cf. SEFEHS). The loss in detail is justified by the otherwise prohibitive size of the dataset. For comparison of feeding guilds and ecomorphotypes, however, it would be preferable to group the prey taxa based only on their functional attributes – size, lifestyle (sessile/colonial, burrowing, free swimming, etc.) and self-preservation. Unfortunately this is often simply not possible because these characteristics are not known for the vast majority of individual prey taxa. However, grouping by taxonomy can lead to grouping species with quite different ecological roles.

Pooled phyla such as polychaetes or gastropods, for example, contain species with very distinct stable isotope ratios that reflect their very different feeding levels.

So it is perhaps not surprising that ecomorphotypes do not necessarily reflect traditional feeding guilds. We have in effect two different views of fish trophodynamics, because the two analytical techniques aggregate the data in different ways (taxonomic or functional).

Multivariate analyses of dietary data and ecomorphotype characters provide different aggregations of species, although there is substantial crossover. Dietary analyses have the advantage of being direct (though time-limited) measures of interaction, and would have obvious advantages in a system dominated by predation on species of interest. This does not seem to be the case presently on the southeast Australian shelf and the ability to predict interactions of fish species based on competitive interactions is low (Bax 1999). We suggest, therefore, that ecomorphotypes, which are based on feeding and locomotive functions, may provide a more useful view of this system than dietary guilds, which cover competition in (or adaption to) both feeding and habitat overlaps.

Indirect trophodynamic grouping using stable isotopes

Stable isotope ratios in the tissue of organisms are indirect mean of determining the trophic level and dietary composition of the organism (Abend and Smith 1997). As with diet analysis, there was not much overlap between ecomorphotype groupings and stable isotope signatures in the SEFEHS study. The shelf ecosystem in this area is driven by pelagic production (FRDC report 94/040), while stable isotopes show only trophic level, which is a very coarse measure. More interestingly, stable isotope signatures were not closely related to any particular ecomorphotype character, except for gut length – the relationship between longer gut and herbivory is well established in the literature.

The differences between grouping by ecomorphology and either direct or indirect trophodynamics suggests that diet is not a ecological process that is easy to describe from morphology alone.

Species assemblages

In the SEFEHS, habitats were identified from on species assemblages. Recoding of the species in each habitat to ecomorphotypes aggregated 7 habitats, or species assemblages, into 2 ecomorphotype assemblages. On the inner and outer shelves the distributions of ecomorphotypes in the northern and southern regions are similar, despite their different taxonomic composition. On the mid-shelf, however, the distribution of ecomorphotypes in the northern and southern regions does differ. The northeastern mid-shelf is comparable to the outer shelf areas, while the southwestern mid-shelf resembles the inner shelf areas. This is probably because the narrow middle shelf in the northern region is close to the shelf break, while in the southern region it is some distance from the shelf break. Thus the mid-shelf ecomorphotype community emphasises the ecological processes of shelf-break proximity. Community structure based on taxonomy, however, shows the middle shelf in the north and south to differ and to be distinct from the inner and outer shelf communities (FRDC Report 94/040).

The similarity in the community structure of the southern and northern regions, as described by ecomorphotypes, is especially illustrative of the power of the ecomorphotype analysis. The

northern and southern regions of the study area (part of the South Eastern Biotone) are associated with different provinces in the IMCRA Bioregion analysis – Central Eastern Province fish in the northern region; Tasmanian or Bassian Province in the southern region. Whereas the IMCRA Bioregion analysis detects a difference between the Central Eastern, Tasmanian and Bassian provinces based only on taxonomy (with associated importance for biodiversity), ecomorphotype analysis shows the similarity in community structure between the regions (with associated importance for ecological processes and sustainability).

5.4.2 Managing Sustainability and Biodiversity

Australia has taken the first scientific steps in managing its marine environment for sustainability and biodiversity, with a process to reduce the overall complexity by defining particular bioregions assumed to represent functionally independent areas. The Interim Marine and Coastal Regionalisation for Australia (IMCRA Technical Group. 1997) identifies biological and physical boundaries between marine environments to assist in planning biodiversity conservation and sustainable development. Demersal/pelagic provinces and biotones were based on a classification of demersal/pelagic fish species diversity and richness. This classification is considered essential for identifying an ecologically or biogeographically representative system of protected areas. But where within each bioregion would a protected area, or system of protected areas, be placed, and how would this decision be made? A rapid assessment technique was required that could define ecologically meaningful areas within bioregions.

Definition of demersal provinces and biotones was based on a classification of demersal species diversity and richness. The basic unit was therefore species. Obviously species is the appropriate unit to use to measure biodiversity – once corrections for taxonomic relatedness have been made (Warwick and Clarke 1995). But bioregionalisation is a process developed in response to Australia's commitment to protection of marine biodiversity AND ecological processes, AND to the sustainable use of marine resources (IMCRA Technical Group. 1997). How well does biodiversity relate to ecological processes? What is the relationship between biodiversity and sustainability?

In this project we have attempted to develop a classification of the fish component of the southeast Australia shelf ecosystem that is based not on species, but instead directly on ecological processes. In this way we hope to provide a clearer relationship between fish communities and sustainability (at the system level) than could be provided by an assessment of species abundance, or biodiversity alone. By integrating the data to a level higher than individual species we also have attempted to develop a rapid assessment technique that could be applied to assess fish communities and their ecological role in the absence of detailed taxonomic, habitat, and dietary data.

We described 20 ecomorphotypes for the southeast Australian shelf ecosystem. Each ecomorphotype contained from 1 to 23 species, although these numbers are underestimates as we only categorised 114 species out of ~230 caught during the SEFEHS project, and 411 species have been recorded as likely in the study area. Ecomorphotypes were developed through aggregating species into distinct functional groups based on their morphological adaptation to locomotion, feeding and self-preservation, although self-preservations was not found to be useful axis for aggregation. The final 20 ecomorphotypes represent unique

combinations of the locomotion and feeding functional groups (out of a possible 75). These ecomorphotypes are quite stable:

- They bear considerable resemblance to the morphotypes described through aggregation of the entire data set;
- They can be recovered from a reduced dataset (21 measurements and 18 coded characters)
- The ecomorphotypes can be named – i.e. they represent groups with distinct ecological characteristics

Furthermore, if ecomorphotypes do provide a reasonable classification of functional groups within an ecosystem, then similar ecomorphotypes should appear in similar ecosystems. As mentioned in Section 4.1.1, the study area is contained within the South Eastern Biotone, an area of overlap between the demersal Central Eastern and the Bassian and Tasmanian Provinces (IMCRA Technical Group. 1997). Provinces were defined as separate ecosystems, based on their species composition. Hence it may be expected that the ecomorphotype distribution is similar within each provinces, as these types are thought to represent functional units within a system.

To test this assumption, we intended to directly compare the ecomorphotype distribution of the provinces, by replacing indicator species by their ecomorphotype. Unfortunately, the demersal fauna regionalisation is mainly based on coastal species (Last CSIRO, pers. comment); comparison of a list of indicator species for these provinces (IMCRA Technical Group. 1997), with the ~230 species caught in the study area, during the SEFEHS study (Bax and Williams 1999) showed an overlap of only few species, none of which were included in the present study. However, as mentioned above, the fact that the north-south distinction made in the SEFEHS habitat study (inferring the influence of the different provinces) is not observed in the ecomorphotype distribution supports the assumption, that separate ecosystems as defined by species do have similar ecomorphotype compositions, hence confirming that ecomorphotypes represent ecosystem functional groups.

Does ecomorphology provide a higher level of conservation unit that addresses more than one of the IMCRA aims – or, does ecomorphology provide additional information to the mapping of bioregions? The IMCRA approach appears to have attained its aim of identifying demersal provinces across the whole shelf, even though the regionalisation was primarily based on coastal species. The evidence of this is in the distinct southwest to northeast cline observed in the species assemblages of all depth ranges (Bax and Williams 1999). However, IMCRA did not identify the depth cline that was observed in both the species and ecomorphotype assemblages in the SEF study area.

Ecomorphology does represent a short-cut to the assessment of community structure, habitat association and ecological processes and hence a useful first step in the management of an area, but it cannot replace a species approach if biodiversity management is the prime objective.

5.4.3 Are ecomorphotypes equally vulnerable?

The 20 defined ecomorphotypes have quite different species numbers. In some ecomorphotypes (such as the eels) this is mostly an artefact of our sampling and species selection, as there are

several other species occurring in the area that would join this ecomorphotype. Other ecomorphotypes, such as those containing whip tails or blue grenadier represent fish from the continental slope that appear in the area due to deep upwelling or are juveniles on their ontogenetic cross-shelf migration. These are intriguing as it suggests that if we were to define slope ecomorphotypes they could represent quite different functional areas than the shelf ecomorphotypes. Other ecomorphotypes with limited species membership may perform very important ecological roles. The Macroramphosidae is one example, where the two species are both numerous, have little overlap in depth range and have a highly adapted mouth that could eat prey that other ecomorphotypes could not use. Current fishing practices are unlikely to impact such numerous groups. Some species-poor ecomorphotypes, may be more vulnerable. – *Squatina australis* and *Callorinchus milii* are two examples of distinct ecomorphotypes that are fished commercially.

In a more general sense, a potential role identified for ecomorphology was to determine/predict which groups or ecomorphotypes might be particularly vulnerable to specific pressures, e.g. intensive fishing, gear types, habitat modification.

Ecomorphotypes as we identified them in the present study are not indicative of vulnerability to fishing. This type of vulnerability depends to a large extent on life history strategy – longevity, growth rate, age at maturity, reproductive strategy (Rochet 1998, Walker and Hislop 1998). Although we identified this as an important ecosystem functional area, we did not include it in our analyses. As we aimed at developing a rapid assessment method, we excluded characters that were difficult to measure, or that depended on seasonally targeted sampling (e.g. gonad/egg size and weight of ripe fish). However, numerous life-traits of fishes are positively correlated with body size (Winemiller and Rose 1992; Sasal *et al.* 1999). As mentioned above, size does not play an important role in the ecomorphotypes and is a factor that should be included additionally to ecomorphology if community processes and management is examined; by including size, certain life history traits would presumably be factored in.

Ecomorphology does hold promises for identifying vulnerability to gear types. The ecomorphotype incorporates shape and locomotion type, thus allowing inferences of their interaction with gear types across species or family groupings. An indication of this is shown in section 5.3.1 where gillnet catches were clearly dominated by ecomorphotypes 18 and 19 – both 'cruisers' that are torpedo shaped, relatively large and are not associated with the bottom, while the trawl catches in similar areas caught a much more diverse set of ecomorphotypes, with a tendency towards more sediment associated groups (types 2 and 8).

Vulnerability to habitat modification may also be inferred from the ecomorphotypes of fishes. In particular, the effect of broad scale habitat modification, like clearing the bottom of epibenthos by intensive trawling, turning a structured habitat into sediment flats (*sensu* Sainsbury *et al.* 1997) could be predicted and/or documented more clearly referring to ecomorphotypes rather than to seemingly independent species.

6 BENEFITS

At the time of application, this project was described as benefiting only the South East Fishery, with benefits within that fishery split 90:10 to commercial and recreation fishers. This seemed appropriate at the time given the most important goal of this project – to develop a rapid-assessment technique that can be used to quickly and effectively describe the primary features of community structure in relation to habitat use and biological interactions between fish species in Australia's fished ecosystems. It was hoped that this would provide information to fisheries managers, enabling them to determine potential indirect biological interactions that could reverse or nullify management interventions.

Fisheries Managed by:	Commercial Sector	Recreational Sector	Other Fisheries Beneficiaries
Australian Fisheries Management Authority AFMA – South East Fishery	90	10	-
Total	90	10	-
Non-Fisheries Beneficiaries			
Summary Flow of Benefits			
Total Commercial Sector Total Recreational Sector Total Other Fisheries Beneficiaries Total Non-Fisheries Beneficiaries			90 10 - -
Summary Flow of Benefits			100

However, as the project developed, the need to develop descriptors of marine ecosystems became more apparent as the next step in the IMCRA Bioregionalisation below the level of Province or Biotone. Furthermore, as a first step in Australia's comprehensive Oceans Policy, the south-east marine domain has been selected as the first region for multi-use, ecosystem-based regional marine planning. A key issue in managing the region and demonstrating the fishery's sustainability is understanding the relative roles of natural processes and human impacts – with imperfect knowledge of either. The rapid assessment process that we have developed provides one way to describe the structure of the ecosystem below the level of Province or Biotone. It therefore provides Australia's environmental managers with a new way

to view marine ecosystems (especially on the shelf off southeast Australia) and develop management strategies at scales appropriate to the scales of ecosystem processes and distributed over space at scales appropriate to ecosystem structure. The importance of this new view of ecosystem structure and processes is especially evident in the resolution provided on structuring of these features with depth. Whereas the IMCRA Bioregionalisation process depicted shelf ecosystems as homogenous within Province or Biotone, it is clear from this work that there are at least 2 (perhaps 3) depth-related communities on the shelf and the extent of these communities depends on the physical and oceanographic structure of the shelf itself.

7 FURTHER DEVELOPMENT

This project has shown the potential of ecomorphology to develop a structural view of a marine ecosystem based on morphological characters and their functional use. Indications from the analyses, where two slope species form separate ecomorphotypes from the shelf ecomorphotypes, are that the slope environment will have different ecomorphotypes and a different representation of described ecomorphotypes. A project similar to this based on slope species would determine those differences, develop a comparable structural view for the slope and improve interpretation of the ecological significance of the determined ecomorphotype structure of the shelf.

Any further ecomorphology studies would profit from developing the analytical techniques developed in this project. In particular, multivariate analyses could be improved, especially by using algorithms that provide confidence levels for multivariate analyses and the probability that individual species are members of the defined group. Randomisation approaches to multivariate analyes are now a real possibility given recent increases in computing power.

This project required development of novel similarity indices. Although we developed one that worked for our data, we are not convinced that we have explored all possible avenues for describing similarity. Further experimentation with weighting values of secondary characters in the similarity measure for hierarchical characters is an obvious area for further research in multivariate analyses.

We defined three functional areas in this analysis of ecomorphology. There is room for further development of the ecomorphotypic concept. One functional area that we were unable to include to our satisfaction was life history, especially growth rates, fecundity, mortality. This area would be especially useful in determining the vulnerability of different species or ecomorphotypes to fishing. A second area that we expected to account for, but may not have done sufficiently, was buoyancy control and implied life style. Addition to or increased emphasis on these functional areas would increase definition in the analyses.

The South East Fishery has been targeting the shelf since the fishery began in 1914. The fish community as it exists today is the consequence of anthropogenic as well as ecological constraints. Further functional areas could be added to, or weighting could be increased on characters important in multiple functional areas, to emphasise the following anthropogenic influences on the fish communities:

- Survivability after commercial fishing (many sharks and puffer fish live for a long time out of the water and may be sent back alive to the sea)

- A generalist or scavenger diet (e.g. dogfish or ling) that would enable the species to profit from discards of dead fish from commercial fishing

Lastly, there is a clear need to continue the discussion developed in this project on what are the suitable frameworks from which to view and understand marine ecosystems. We believe that the combination of ecomorphology and size would provide powerful descriptors of the dynamics and interactions of fish species in marine ecosystems. This and other frameworks should be explored, because our understanding of how marine ecosystems function and

therefore what are the appropriate approaches for their management, are critically dependent on the framework within which we view them.

8 CONCLUSIONS

"Wherever the reign of nature is not disturbed by human interference the different plant-species join together in communities, each of which has a characteristic form, and constitutes a feature in the landscape of which it is a part. The reason for their living together does not lie in their being of common origin, but in the nature of the habitat. They are forced into companionship not by any affinity to one another but by the fact that their vital necessities are the same.... [D]ifferent species with similar needs may flourish undisturbed side be side as men live together in one house or in one town, and, although their customs and their needs may not be exactly the same, yet form a society which is permanent and thrives, and wherein each member feels at home, because it rests upon the common usages and is adapted to the local conditions." (Kerner, 1897, 885)

"The question of the actual complexity of the dynamics of natural communities is one of the major problems of contemporary population biology." (Godfray and Blythe 1990)

"If the Lord Almighty had consulted me before embarking on creation I should have recommended something simpler" Attributed to Alphonso X the Wise (1221-1284), King of Castile and Leon.

The ideas of form and function, adaptation and habitat, have been around for many years, especially in terrestrial environments (e.g. Kerner 1897), where we take for granted that particular plants are adapted to particular soils and environmental conditions. In fact, we purposely change terrestrial habitats so that plants and animals adapted to different habitats can thrive in them.

Our ability to change freshwater aquatic environments to benefit particular species is limited; in marine environments it is practically non-existent. The main reason is that we do not understand how the structure of species and communities is linked with their function. Models of aquatic communities have typically taken a reductionist approach based on species or size classes and only rarely both (see review in Bax 1999), hence the prevailing emphasis on assessment and management of single species. Attempts to move to a more holistic view of marine ecosystems have typically been extensions of the reductionist approach using units of species and their interactions; only rarely have they attempted to look for more general system attributes. Are the units of species or size class the relevant units to understand and manage aquatic processes? Do they provide the correct system view? Is there indeed a correct view or does this depend on the interests of the observer? While the system view constructed from individual species has obvious social and economic relevance, its relevance to sustainability of the system, and therefore over the long-term the species themselves, is far less certain.

Ecomorphology returns us to the basic elements of ecology – how individual components of an organism either adapt it to, or restrict it from, particular ecological roles. This is the knowledge that enables us to manipulate and manage terrestrial environments at many levels, but has rarely been described for aquatic communities. If these elemental truths are found, there is the potential to understand the structure and infer the dynamics of aquatic communities. Through this understanding, we can hope to view aquatic systems abstractly, and at a level of simplicity that can be used in modelling and management for long-term sustainability.

There have been numerous ecomorphology studies of fishes; however, until now this discipline has rarely been applied to the temperate marine environment. Most studies have concentrated either on species within one family, or communities with restricted species or extent (e.g. Schiemer and Wieser 1992; Motta *et al.* 1995a; Winemiller *et al.* 1995; Labropoulou and Markakis 1998; Piet 1998, Platell *et al.* 1998). While some functional systems such as digestion, vision and foraging are well studied, others such as locomotion or electroreception have received little attention (*sensu* Norton *et al.* 1995).

The present study is unique in that it targeted a wide variety of temperate marine fishes – 114 species in 53 families – and characters (*Objective 1: Measure the functional morphology of 50 prevalent species (including quota species) in the SEF shelf trawl fishery, including internal and external features*). Unlike many previous studies, we did not concentrate on one particular feature and its function, but instead chose a 'shot gun' approach, measuring and coding a wide variety of morphological features purported to relate ecological function. This approach was better suited to determine the features that define guild or community structure in a large marine ecosystem with high species richness – particularly as we proposed to develop a rapid assessment procedure from the results of this study.

This project has provided answers (and questions) at three levels. First, we developed a conceptual approach, supported by a rigorous statistical framework to determine the primary functional groupings or "ecomorphotypes" found on the southeast Australian shelf. Second, we used these ecomorphotypes to define, compare and contrast the functional characteristics of the main fish communities in this area as defined by geography, depth, habitat and diet (*Objective 2: Analyse these morphological features to determine the structure of species assemblages, habitat use, and potential biological interactions*). Third, and perhaps most importantly, the project contributes to the process of determining what necessarily arbitrary representation, or view, of a marine ecosystem provides useful information on how the system functions. For it is clear that there are many alternative views of a marine ecosystem. Aggregation of information based on taxonomic distinctness, fish communities, diet or habitat use are just a few of the more obvious methods of data reduction used to provide a tractable view of a complex, multidimensional system. However, as "the conceptual picture which we form about ecological objects . . . is dependent on our perception of their similarities."(Orloci 1978), it is clear that we need to be aware that any particular aggregation or data reduction method is a caricature of a complex reality and the simplification will have particular implications for our understanding and management approach.

We defined 20 ecomorphotypes based on their different adaptations for the functions of locomotion, feeding and self-preservation. Each ecomporphotype contained between 1 and 23 species, although this is an underestimate, as we categorised only 114 out of the ~230 species caught at the same time in this area. These ecomorphotypes are stable, can be recovered from a reduced data-set and can be named – that is, they represent groups of fish with distinct ecological characteristics. The relative distribution of ecomorphotypes was consistent between the north and south of the study area (which represent Central Eastern and the Bassian or Tasmanian Provinces), indicating that we have defined functional units that are common between ecosystems (as defined by the IMCRA Technical Group 1997). At the same time ecomorphotypes define quite different communities on the inner and outer shelf, with the middle shelf communities being more similar to the outer shelf community when the shelf is narrow, but more similar to the inner shelf when the shelf is extensive. This provides community classification on an axis that was not considered in the IMCRA Bioregionalisation.

The distribution of ecomorphotypes varied according to habitat type. For example strongly compressed fish, often with inferior or protrusible (even tubular mouths) specialised for ram and suction feeding, were found on sediment flats; while large, discoid-bodied ecomorphotypes with well-developed teeth for feeding on hard-bodied prey were associated with reef. Thus, ecomorphology analytically identified what an experienced observer familiar with the fishery would class as sediment flat and reef fishes. Inbetween these habitats, ecomorphotypes of benthopelagic cruising ram-suction feeders, prevailed, along with slower fish protected by body armouring. (*Objective 3: Compare the information on community structure, habitat use and biological interactions derived in this study against independent information on habitat use, water column distribution and diet, to determine which morphological features provide useful information on the fishes ecological role*).

There was less correspondence between ecomorphotypes and trophic guilds determined from diet. This is at least partly due to prey species with quite different functional attributes being aggregated before the trophic guild analysis. Ideally, grouping of prey species before their analysis would be based on their ecology and behaviour, rather than their taxonomic affinity. Such data are rarely available however, and ecomorphology provides an alternative view of trophic interactions in this instance, incorporating both diet and habitat use.

One of the aims of this project was to develop a rapid assessment approach to describing ecologically important features of marine ecosystems. (*Objective 4: Ascertain the potential of functional morphology to provide rapidly and efficiently the information on species interactions, habitat use, and susceptibility to fishing gears, that is essential to fishery management using ESD principles*). The stability of ecomorphotypes derived from the reduced character set suggests that this is possible. Rapid definition of ecomorphotypes can be achieved from only 21 measurements and 18 coded characters for each species. However, ecomorphotype definition at this level may still not be a truly rapid assessment protocol, especially in developing countries where the computer technology is not available. In those situations we believe it would be possible for trained observers to assess the presence of indicative ecomorphotypes from viewing unsorted catches. In this manner the habitats and dominating physical and ecological processes impacting fish communities could be determined from observing the functional adaptations of the fish caught in the area.

Ecomorphology provides a short-cut to assessing community structure, habitat association and ecological process, and hence a useful first step in the management of an area. It does not replace taxonomic-based classifications when biodiversity is the primary concern, but may provide a better response to Australia's commitment to protection of biodiversity, ecological processes and sustainable use of marine resources than taxonomic classification alone.

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APPENDIX 1: INTELLECTUAL PROPERTY

The intellectual property arising from this work is the property of both CSIRO and FRDC.

APPENDIX 2: STAFF

Nic Bax	CSOF6	Principal Investigator – Project Leader
Alan Williams	CSOF5	Co-Principal Investigator – Taxonomist/Ecologist
Franziska Althaus	CSOF3	Morphometrics/Data Analysis

We have benefited from discussions with Peter Last (CSIRO) on fish taxonomy, form and function and with Leigh Belbin (Antarctic Division) on multivariate approaches to data analysis.

APPENDIX 3: TEST OF SIZE ACCOMMODATION IN MDS

A data subset for *Genypterus blacodes* (ln-standardised) has been analysed with a MDS (Bray-Curtis). The dimension scores have then been regressed against standard length (SL) to determine if one axis highly correlates to SL, similarly to the first axis in PCA

1st Dimension

Dep Var: DIM(1) N: 13 Multiple R: 0.012 Squared multiple R: 0.000; Adjusted squared multiple R: 0.0 Standard error of estimate: 0.654

Effect	Coefficient	Std Error	Std.Coef	Tolerance	t	P(2 Tail)
CONSTANT	-0.077	1.970	0.0	.	-0.039	0.970
SL	0.019	0.483	0.012	1.000	0.039	0.969

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	0.001	1	0.001	0.002	0.969
Residual	4.710	11	0.428		

Durbin-Watson D Statistic	2.862
First Order Autocorrelation	-0.436

2nd Dimension

Dep Var: DIM(2) N: 13 Multiple R: 0.054 Squared multiple R: 0.003; Adjusted squared multiple R: 0.0 Standard error of estimate: 0.626

Effect	Coefficient	Std Error	Std.Coef	Tolerance	t	P(2 Tail)
CONSTANT	-0.338	1.885	0.0	.	-0.179	0.861
SL	0.083	0.462	0.054	1.000	0.180	0.860

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	0.013	1	0.013	0.032	0.860
Residual	4.314	11	0.392		

Durbin-Watson D Statistic	2.975
First Order Autocorrelation	-0.496

3rd Dimension

Dep Var: DIM(3) N: 13 Multiple R: 0.020 Squared multiple R: 0.000 Adjusted squared multiple R: 0.0 Standard error of estimate: 0.600

Effect	Coefficient	Std Error	Std.Coef	Tolerance	t	P(2 Tail)
CONSTANT	0.117	1.806	0.0	.	0.065	0.950
SL	-0.029	0.443	-0.020	1.000	-0.065	0.949

Analysis of Variance

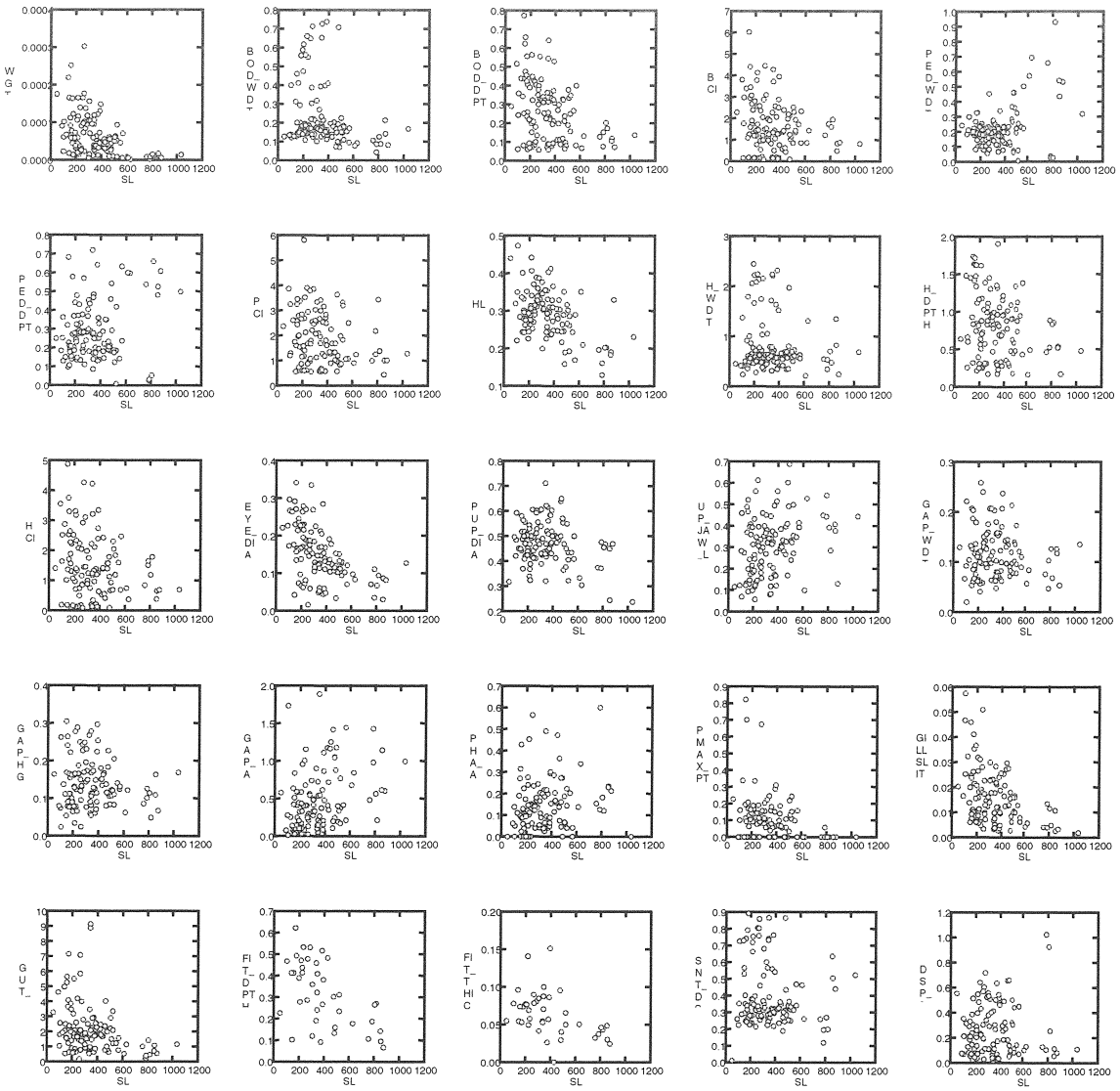
Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	0.002	1	0.002	0.004	0.949
Residual	3.961	11	0.360		

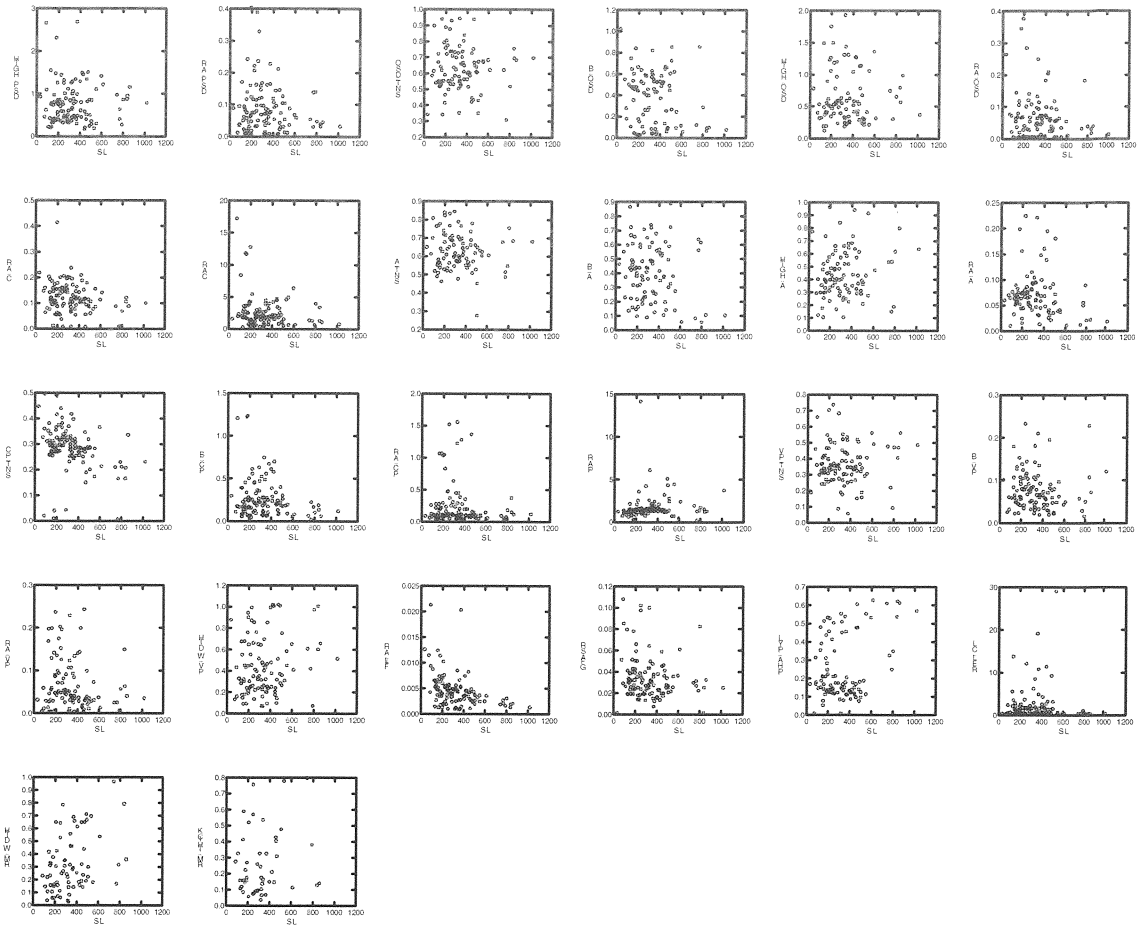
Durbin-Watson D Statistic	3.002
First Order Autocorrelation	-0.517

No significant correlation between standard length and any of the three MDS-dimensions was found. Hence, MDS on ln-transformed data does not allow for accommodation of size differences without standardising for this factor.

APPENDIX 4: SIZE DEPENDENCE OF CHARACTER VALUES

Scatterplots of all standardised measurements vs. standard length for 1 fish per species





APPENDIX 5: CHARACTER-SET OF EACH OF THE ANALYSES

all variables used in the analysis	Locomotion	Feeding	Self-Preservation (excl. Locomotion)	Self-Preservation	20 Ecomorphotypes Reduced Data-Set
mfl	L	F	SP	SPL	
sl					
bl					
abdom	L			SPL	
wgt	L				
bod_wdth	L		SP	SPL	X
bod_dpth	L		SP	SPL	X
BCI	L		SP	SPL	X
ped_wdth	L				
ped_SHP	L			SPL	
ped_dpth	L			SPL	X
PCI	L				X
col_dors			SP	SPL	
col_vent			SP	SPL	
cntr_shd			SP	SPL	
bod_pat			SP	SPL	
hl		F			
h_wdth		F			X
h_dpth		F			X
HCI		F			X
eye_mob	L		SP	SPL	
eye_sup			SP	SPL	
eye_pos	L		SP	SPL	
eye_diam		F	SP	SPL	X
pup_diam		F	SP	SPL	
mth_pos		F			X
tub_snt		F			
mth_ang		F			
up_jaw_l		F			X
Max_ext		F			
gap_wdth		F			X
gap_hgth		F			X
gap_ar		F			X
pha_ar		F			
tng_dev		F			
pmax_ptr		F			X
lip_uj		F			
lip_lj		F			
nostril		F	SP	SPL	
nas_tent		F	SP	SPL	
Gust_app		F	SP	SPL	
gillslit		F			X
opercle		F			
finlet	L				
keel	L				
gut_l		F			
fit_dpth	L				
fit_thick	L			SPL	
HSP_P		F	SP	SPL	
hsp_dev		F	SP	SPL	

all variables used in the analysis	Locomotion	Feeding	Self-Preservation (excl. Locomotion)	Self-Preservation	20 Ecomorphotypes Reduced Data-Set
hsp_no		F	SP	SPL	
LL_P		F	SP	SPL	
LL_dev		F	SP	SPL	
ll_brnch		F	SP	SPL	
ll_scl		F	SP	SPL	
SCL_P	L		SP	SPL	
scl_sz	L		SP	SPL	
scl_H			SP	SPL	
scl_vent			SP	SPL	
scl_overlp	L				
scl_form	L		SP	SPL	
BSP_P		F	SP	SPL	
bspr_dev		F	SP	SPL	
bsp_no		F	SP	SPL	
DSP_P	L		SP	SPL	
dsp_sc	L				
dsp_rig	L			SPL	
dsp_col	L				X
d_shp			SP	SPL	
snt_dsp	L			SPL	
dsp_b	L			SPL	X
dsp_hgth	L		SP	SPL	
dsp_ar	L			SPL	
dso_P	L			SPL	
dso_sc	L				
dso_rig	L			SPL	
dso_col	L				
snt_dso	L			SPL	
dso_b	L			SPL	
dso_hgth	L			SPL	
dso_ar	L			SPL	
c_P	L			SPL	
c_sc	L				
c_rig	L				
c_col	L				X
c_shp	L				
c_ar	L				
CAR	L			SPL	
a_P	L			SPL	
a_sc	L				
a_rig	L			SPL	
a_col	L				X
snt_a	L			SPL	
a_b	L				
a_hgth	L			SPL	
a_ar	L			SPL	
pc_P	L			SPL	
pc_sc	L			SPL	
pc_rig	L				
pc_col	L				X
pc_tact		F			
pc_loco	L				X
pc_pos	L			SPL	X
pec_ang	L			SPL	X

all variables used in the analysis	Locomotion	Feeding	Self-Preservation (excl. Locomotion)	Self-Preservation	20 Ecomorphotypes Reduced Data-Set
pc_shp	L			SPL	
snt_pc	L				
pc_b	L			SPL	X
pc_ar	L			SPL	X
PAR	L			SPL	
pv_P	L			SPL	
pv_sc	L				
pv_sh	L				
pv_rig	L				
pv_col	L				X
pv_tact		F			
pv_pos	L			SPL	
snt_pv	L				
pv_b	L				
pv_ar	L			SPL	
pv_wdth			SP	SPL	
Mth_tth		F			X
Pha_tth		F			X
rak_P		F			
rak_cat		F			
rak_sp		F			
rak_flex		F			
rak_tp		F			
rak_lon		F			
rak_ar		F			
GRAsR		F			
fil_P	L				
fil_sp	L				
fil_flex	L				
fil_lon	L				
fil_ar	L				
GFAsR	L				
SB	L				
sb_dev	L				
sb_vol	L				
PYL_P		F			
pha_pyl		F			
pyl_caec		F			
rel_CL		F			X
RM_P	L				
rm_ptch	L				
rm_row	L				
rm_cont	L				
rm_dev	L				
rm_wdth	L				
rm_thick	L				