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SPECIES AND STOCK DELINEATION IN AUSTRALASIAN OREOS (OREOSOMATIDAE)

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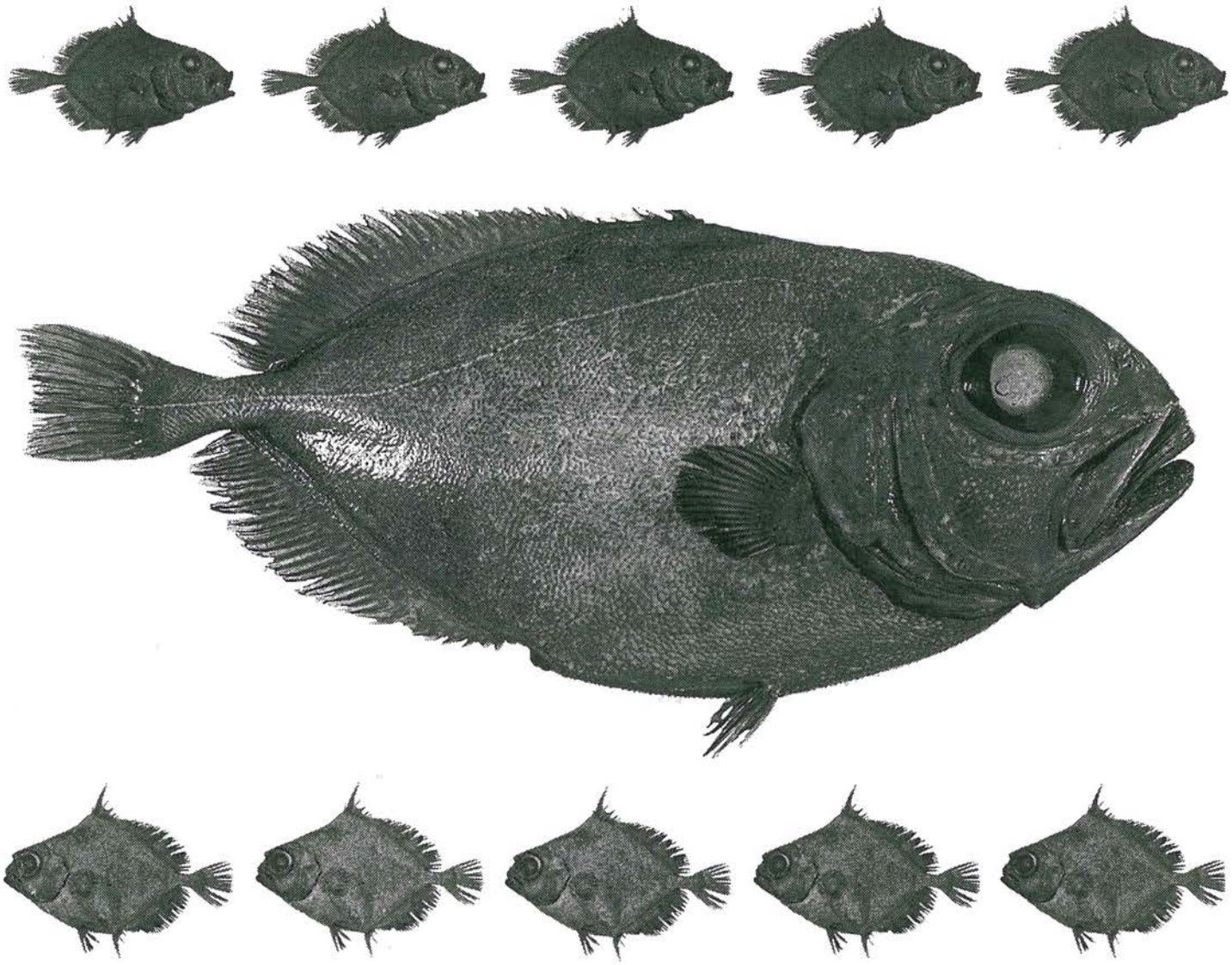

CSIRO AUSTRALIA

DIVISION OF FISHERIES

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(Oreosomatidae)

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Species and Stock Delineation in Australasian Oreos (Oreosomatidae)

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1. NON-TECHNICAL SUMMARY

Oreos (family Oreosomatidae) are now an important component of the South East Fishery, but little is known of their basic biology. Prior to this project, five species of oreo had been identified from Australasian waters: black oreo (*Allocyttus niger*), warty oreo (*Allocyttus verrucosus*), spikey oreo (*Neocyttus rhomboidalis*), oxeye oreo (*Oreosoma atlanticum*) and smooth oreo (*Pseudocyttus maculatus*). During this project, a sixth oreo was identified, the rough oreo (*Neocyttus* sp. A). Identification of oreos in past surveys and in log books has not always been reliable; here a diagnosis of all known Australasian species (including the endemic rough oreo) is provided to enable accurate identification in future surveys.

Reliable sources of oreo identification were summarised to provide maps of the likely distributions of oreos in Australasian waters. The greatest commercial quantities occur locally on seamounts and on the upper continental slope in cool temperate areas. Consequently, any additional undiscovered stocks of oreos are likely to occur south of the Australian mainland, possibly on seamounts.

Single large samples of the four main commercial oreo species (black, warty, spikey and smooth) were analysed for genetic variation using both allozyme and mitochondrial DNA approaches in order to establish base-line levels of variation. Allozyme variability for each of these species was high in relation to most other teleosts; mtDNA variability was typical of teleosts. These assessments of genetic variability were taken early on in the development of the oreo fishery, and will be monitored at irregular intervals to examine whether fishing pressures affect levels of genetic variation.

A phylogenetic analysis of the relationships of the six Australasian species along with a North Atlantic species (the false boarfish, *Neocyttus helgae*) was carried out using the allozyme data and outgroup species from three families with possible evolutionary links to oreos: Acanthuridae, Berycidae and Zeidae. The oxeye oreo was found to be the most divergent oreo, and the spikey oreo and the false boarfish found to be the most closely related. There was little evidence to support the current inclusion of black and warty oreos in the same genus. Generic placements need to be reevaluated using a combination of genetic and morphological techniques.

Stock structures of the four commercial oreo species were assessed using genetic (allozyme and mitochondrial DNA) and morphological (counts of fin rays, lateral line scales and pyloric caeca, and in the case of spikey oreos, morphometric analyses of body shape) approaches. The conclusions were:

Black oreos: the New Zealand sample appeared to constitute a stock distinct from the Australian (southern Tasmania, Western Australia) stock. This conclusion is based on a small but significant difference in mtDNA haplotype frequencies (with no detected allozyme differences), supported by differences in pyloric caeca and lateral line scale counts.

Smooth oreos: there was no genetic evidence of stock structuring, with only lateral line scale counts distinguishing a Western Australia sample from southern Tasmanian, Lord Howe Rise, and New Zealand samples. This should be seen as only suggestive of stock heterogeneity.

Warty oreos: no New Zealand sample was forthcoming, but allele frequencies at the allozyme locus *MPI** differentiated a southern Tasmanian sample from samples from Western Australia and New South Wales, providing weak evidence of two stocks. Differences in dorsal-fin ray counts and lateral line scales suggest that a Lord Howe Rise sample might be from a third stock.

Spikey oreos: two depth-separated races were detected, primarily distinguishable by striking differences in *sSOD** allele frequencies. Three stocks of the deep-water race (>700 m) were identified: Western Australia (distinguished by *MPI**); New Zealand (distinguished by *MPI** and *PGM-1**); and southern Tasmania, East Tasmania sample 1, New South Wales and Lord Howe Rise. There was no evidence for the shallow-water samples (<700 m) (East Tasmania samples 2 and 3, West Tasmania, and South Australia) constituting more than a single stock.

Future work could include the examination of additional fish, both to increase sample sizes from existing areas and to sample new areas, and the development of additional genetic markers. A recently discovered class of genetic marker, DNA microsatellites, has shown promise in delineating populations of marine teleosts that could not be separated by allozyme nor mitochondrial DNA analyses, and should be developed and applied for a more powerful examination of genetic stock structures in oreos.

2. BACKGROUND

Oreos (family Oreosomatidae), or oreo dories, are found in deepwater (400–1500 m) over the continental slopes and seamounts of most temperate, and some tropical and subtropical, regions world-wide. They appear to be more diverse and more abundant in the Southern Hemisphere, but it is unclear whether the relatively high abundance in the south reflects a real biomass difference or a greater deepwater trawling effort in the Australasian region.

The family contains four genera and over ten species (Heemstra, 1990, and see Table 2.1). Prior to this study, five had been recorded from Australasian waters: *Allocyttus verrucosus* (warty oreo), *A. niger* (black oreo), *Neocyttus rhomboidalis* (spikey oreo), *Oreosoma atlanticum* (oxeye oreo) and *Pseudocyttus maculatus* (smooth oreo). However, the identity of a number of CSIRO and other museum specimens had yet to be determined.

Oreos are amongst the most abundant bentho-pelagic fishes on the mid-continental slope. Other oreos recorded from the Southern Hemisphere are *N. acanthorhynchus* (Indian Ocean) and *A. guineensis* (southern Atlantic and Indian Oceans). Two species, *A. folletti* (North Pacific) and *N. helgae* (North Atlantic), are recorded only from the Northern Hemisphere. Although adults of only one species have been recorded from the North Pacific (records of *A. verrucosus* from this region are referable to *A. folletti*), juveniles of a second unidentified species have been taken off Hawaii.

Commercial landings of oreos from New Zealand waters preceded those from Australia. Indeed, the New Zealand offshore trawl fishery is one of the oldest deepwater fisheries, having been initiated by Russian trawlers in the early 1970s, with a change to a predominately New Zealand catch from 1988-89 (Anon. 1994). In New Zealand, the main oreo fishery is on the Chatham Rise, with the main commercial species being the smooth and black oreos. This fishery has shown a decline in average catch size and it is estimated that the 1993 biomass estimate was 15% of the virgin or unexploited biomass (Anon. 1994). The peak New Zealand oreo catch was 26 500 t in 1981-82; the total catch for 1992-93 was about 23 820 t (Anon. 1994).

In Australian waters, oreos have been principally caught as a bycatch of the deepwater fisheries for orange roughy (*Hoplostethus atlanticus*) and blue grenadier (*Macruronus novaezelandiae*) and were generally discarded. However, the recent reductions in orange roughy catch limits, the development of new fishing grounds off southern Tasmania, and growing market awareness, have resulted in increased targeting of oreo aggregations and a rapid growth and retention of Australian oreo catches (Lyle *et al.*, 1992).

The retained oreo catch from the South East Fishery (SEF) was less than 100 t per annum before 1987, around 2 000 t in 1990 and 1991, over 3 000 t in 1992, and over 1 000 t in 1993 and 1994 (AFMA statistics, unpublished). Actual catches will be higher due to non-reporting and discarding. As in New Zealand, smooth and black oreos

dominate the catch, with smooth oreos being the preferred species and constituting about 95% of the retained catch (Lyle *et al.*, 1992). Catches of spikey and warty oreos are small, while oxeye oreos are still less abundant and are generally discarded because of their small size and low commercial value. It should be noted that both black and warty oreos are correctly marketed as black oreos (Anon, 1995a). The bulk of the smooth and black oreo are caught in depths of 800-1000 m, by vessels which primarily target orange roughy. Warty oreos make up an incidental component of this catch. Spikey oreos are also sometimes caught by orange roughy fishers but are more usually caught in shallower water by vessels fishing the continental shelf and upper slope.

The recent development of the oreo fishery brings with it the need for management on a sustainable basis. This requires information on biology, distribution, stock structure, productivity, and biomass, and only in the last few years have these topics been investigated. A pertinent example of the lack of information is the use of various common names by fishers and managers. Many fishers incorrectly refer to spikey oreos as oxeye oreos (oxeye oreos are, in fact, too small to be of commercial value) and to black oreos as spikey oreos. This has caused confusion in fishery statistics to the extent where oxeye oreos are listed as a species over which the Commonwealth has jurisdiction (Anon 1995b). This current Report is primarily concerned with identification, distribution and stock structure issues, but some relevant findings from other studies are given below.

Spawning for smooth and black oreos off Tasmania is in November and December, and while both species aggregate to spawn, there does not appear to be a single major spawning site as there is for orange roughy (Lyle *et al.*, 1992). Less is known about warty and spikey oreos, although there is evidence of spawning in May-June and September-October respectively. Fertilised eggs are positively buoyant and rise in the water column. Juveniles are pelagic and therefore rarely taken. They differ markedly from adults, so much so that adult and juvenile oxeye were described as separate species, as were adult and juvenile smooth oreo. Juveniles of most species have a greatly enlarged abdomen, bearing one or two rows of cones, protuberances or warts.

Like orange roughy, oreos appear to be extremely long lived and slow growing. This of course reduces the potential productivity of the stock and has important implications for management. Both otolith increment counts and otolith radiometric analysis suggest that warty oreos have a maximum age, for fish of around 34-36 cm, of 130 yr, and that age at maturity for males is reached at around 24 yr and at around 30 yr for females (Stewart *et al.*, 1995). Male and female smooth oreo are estimated to mature at the age of 20-40 yr (Stewart and Smith, unpublished; Doonan *et al.*, 1995), with a maximum age estimated at 86 yr (51.3 cm TL fish, Annala 1995) to 90 yr (52.0 cm, Stewart and Smith, unpublished). Black oreo are estimated to have a maximum age of 120 (42.6 cm fish, Stewart and Smith, unpublished) to 153 yr (45.5 cm TL fish, Annala 1995). Preliminary examination of a small number of spikey oreo otoliths assigned an age of 95 yr to a fish of 41.8 cm (Stewart and Smith, unpublished). Otolith

ageing suggests that growth is relatively rapid for the first few years, with the pelagic juvenile phase lasting some 4 to 6 yr for both smooth and black oreos (Annala 1995; Stewart and Smith, unpublished).

The conservation of biodiversity, both in terms of numbers of species and the genetic diversity contained within them, is a central tenet of the Commonwealth's Ecologically Sustainable Development strategy. Fishing activities can affect species compositions of exploited communities, either directly (by differentially removing targeted species) or indirectly (by, for example, trawling affecting the structure of epibenthic communities). Fishing activities could also be affecting the genetic diversity of exploited fishes. Genetic variation will be lost as population size declines, although it has been estimated that collapsed stocks of commercially important pelagic species which subsequently recover are probably of the order of 1 000 000 individuals (Beverton, 1990). Hence the loss of genetic variation brought about by inbreeding and genetic drift in targeted marine fish is likely to be quite small, although this will depend on spatial structure and local effective population sizes.

More importantly, the size-selective nature of fishing imposes additional selective forces on fish populations and a genetic response is to be expected. The nature of this response is generally hard to ascertain, but a significant decrease in the genetic diversity of New Zealand orange roughy populations (as assessed by allozyme electrophoresis) during a period of severe fishery-led biomass reduction has been recorded (Smith, Francis and McVeagh, 1990). This was attributed to fishing activities differentially removing the largest and more variable or heterozygous fish, although no evidence was advanced to show that the larger fish were indeed more heterozygous. A subsequent study (Ward and Elliott, 1993) found little evidence for any relationship between size and single or multi-locus heterozygosity in orange roughy. No reduction in heterozygosity of Hawaiian spiny lobster (*Panulirus marginatus*) populations was observed following an increase in fishing pressure (Seeb *et al.*, 1990). It should be noted, however, that orange roughy exhibits far more genetic variation than the spiny lobster, and a change in heterozygosity is more likely to be detectable in the former species. The generality of the phenomenon observed by Smith *et al.* (1990) remains unknown; if widespread, then it means that size selective fishing has a more deleterious impact on genetic variation than the small stochastic reduction in variation brought about by a decrease in population size. The development of the oreo fishery provides a rare opportunity to monitor any possible impacts of fishing on genetic variation as the fishery changes from a relatively unexploited to exploited state.

Table 2.1. Oreosomatids of the world. Scientific names of Australasian species are in bold. Abbreviations are as follows: Aus.—Australia; BMNH—British Museum of Natural History; IOAN—Institute of Oceanology, Russian Academy of Sciences, Moscow; juv.—juveniles; Lit.—literature records; MNHN—Muséum National d'Histoire Naturelle; NZ—New Zealand; N—northern; NMNZ—National Museum of New Zealand; SAM—South African Museum; SE—south eastern, *etc.*; spec.—unpublished museum specimen data; ZIL—Zoological Institute of St Petersburg, Russian Academy of Sciences.

Sources were: Heemstra (1990), James, *et al.* (1988), Karrer (1990), Lyle and Ford (1993), Miller (1993), Shcherbachev (1987), Shimizu (1983), and museum specimens.

§ Depth data for specimens examined is only included where it differs from literature records.
* Description of *Neocyttus* sp. A is in preparation (Yearsley and Last)
† Juveniles are pelagic, sometimes taken over deep water
1 Voucher specimen CSIRO H2865.01
2 Voucher specimen IOAN P15776
• A second *Pseudocyttus* species, *P. nemetoi* (Abe, 1957), was recently resurrected by Miller (1993). Further specimens are required to validate *P. nemetoi*.

Scientific name	Author(s)	Synonym(s)	Distribution of adults	Depth[§]	Holotype	Type locality	Common name(s)	Australian marketing name
Allocyttus folletti	Myers, 1960	—	N Pacific	360–740 m	Stanford University 15377	off Eel River, California, USA	oxeye oreo (USA)	—
Allocyttus guineensis	Trunov & Kukuev *in* Trunov, 1982	—	SE Atlantic, SE Indian	230—1130 m, possibly midwater	ZIL 45501	off Angola (SE Atlantic),	—	—
Allocyttus niger	James, Inada & Nakamura, 1988	—	S Aus. and NZ between about 33°S and 50°S	600–1300 m (Lit.); 510 m (spec.)	NMNZ P15939	Chatham Rise, NZ	black oreo (Aus. and NZ)	black oreo
Allocyttus verrucosus	(Gilchrist, 1906)	*Allocyttus verrucosus* var *propinquus* McCulloch, 1914	circumglobal between about 20°S and 42°S, and N Atlantic	340–1630 m (Lit.); 650 m, midwater trawl (juv.[†])	probably lost (SAM)	off Cape Point, South Africa	warty oreo, warty dory (Aus. and NZ)	black oreo
Neocyttus acanthorhynchus	Regan, 1908	—	Indian, although N records may be of *Neocyttus* sp. B	825–915 m (spec.)	BMNH 1908.3.23.122	off NW coast of Madagascar	—	—
Neocyttus helgae	(Holt & Byrne, 1908)	*Crassispinus granulosus* Maul, 1948	NE Atlantic	1020 m (Lit.); 1150 m (spec.)	BMNH 1910.9.17.1	off Southern Ireland	—	—
Neocyttus rhomboidalis	Gilchrist, 1906	*Neocyttus rhomboidalis* var *gibbosus* McCulloch, 1914	circumglobal between about 24°S and 48°S	200–1120 (Lit.)	SAM 11972	off Cape Point, South Africa	spiky oreo, spiky dory (Aus. and NZ)	spikey oreo
***Neocyttus* sp. A**	undescribed*	—	S Aus. between about 35°S and 47°S	750–1300 m (spec.)	—[1]	—	rough oreo (Aus.)	—
Neocyttus sp. B	undescribed	—	N Indian	875 m (spec.)	—[2]	—	—	—
Oreosoma atlanticum	Cuvier, 1829	*Cyttosoma boops* Gilchrist, 1904; *Oreosoma waitei* Whitley, 1929	almost circumglobal between about 30°S and 45°S	220—1390 m (Lit.); midwater trawls (juv.)	MNHN 2242	Atlantic (possibly 30°S 10°E)	oxeye oreo (Aus. and NZ); oxeye dory (South Africa)	—
Pseudocyttus maculatus	Gilchrist, 1906	—	circumglobal between about 25°S and 54°S, and off Suriname (NW Atlantic)	200–1500 m (Lit.); midwater trawls (juv.)	holotype lost	off Cape Point, South Africa	smooth oreo, smooth dory (Aus. and NZ); round oreo (South Africa)	smooth oreo

3. NEEDS

This project sought to cover four needs:

I. THE NEED FOR ACCURATE IDENTIFICATION OF SPECIES AND RESOLUTION OF TAXONOMIC DIFFICULTIES.

The recorded tonnages of individual oreo species in the SEF are unreliable due to confusion over species identification in catch log-books. Some of the species are difficult to distinguish, and one of the aims of this project was to provide reliable morphological and genetic information for species identification in the SEF and throughout the wider Australasian region, and at the same time resolve outstanding taxonomic issues.

II. THE NEED FOR BETTER INFORMATION ON DISTRIBUTIONAL RANGE IN AUSTRALASIAN WATERS.

Information on this topic, including depth, longitude and latitude information, is scattered among many resources. This project aimed to synthesise this information to provide an overall view of the likely distributions of each of the Australasian oreo species.

III. DETERMINATION OF STOCK STRUCTURES.

Prior to this project, there was no information on the stock structure of oreos, neither here nor in New Zealand. Such information is necessary for effective management, since if different stocks can be shown to exist, then these stocks should be managed independently. Thus a major focus of this project was to collect morphological and genetic data on the different species to provide such information, from both Australian and New Zealand samples.

The morphological data collected were mostly meristic (countable) data, including fin ray counts, lateral line scale counts, and gill raker counts. In addition, for the spikey oreos which showed significant genetic differentiation among samples, morphometric measurements such as various lengths and ratios were also taken.

The genetic data collected described variation in both nuclear DNA (via allozymes) and mitochondrial DNA (mtDNA).

IV. EFFECT OF FISHING ON GENETIC VARIATION.

The final aim was to get good base-line information on levels of genetic variation in unexploited stocks of oreos, by examining both nuclear DNA and mtDNA variation. It is hoped that stocks will be monitored to quantify any possible changes over time.

4. OBJECTIVES

There were four objectives to this study. These, as stated in the original FRDC proposal, are:

1. Identification of species and resolution of taxonomic issues in oreo dories,
2. Determine distributional ranges of oreo dories in Australasian waters,
3. Determine base levels of genetic variability in fish stocks currently subject to low exploitation rates, and
4. Determination of stock structures of oreo dories in Australasian waters.

5. MATERIALS AND METHODS

5.1. SPECIMEN AND SAMPLE ACQUISITION

Two types of specimens were collected: preserved museum specimens for taxonomic analysis and frozen specimens (from which samples were taken) for stock structure analysis.

5.1.1. PRESERVED SPECIMENS (FOR TAXONOMY):

Museum specimens of all recognised oreosomatid species worldwide were required for species verification and comparisons with Australasian material.

Australian material was examined at:

AMS—Australian Museum, Sydney;
CSIRO—CSIRO Division of Fisheries, Hobart;
NMV—Museum of Victoria, Melbourne;
QM—Queensland Museum, Brisbane;
TMAG—Tasmanian Museum and Art Gallery, Hobart;
WAM—Western Australian Museum, Perth.

Overseas specimens were loaned from the following institutions:

BMNH—British Museum of Natural History;
CAS—Californian Academy of Sciences, USA;
IIPB—Instituto de Ciencias del Mar, Spain;
IOAN—Institute of Oceanology, Russian Academy of Sciences;
MNHN—Muséum National D'Histoire Naturelle, France;
SAM—South African Museum;
UW—University of Washington, USA;
ZIL—Zoological Institute of St Petersburg, Russian Academy of Sciences.

The following specimens of stated standard lengths (SL) were examined:

Allocyttus folletti Myers, 1960

Holotype.— not examined

Paratypes.— not examined

Other material (12 specimens).— CAS 26784, 173 mm SL, NE Pacific, off Sonoma County, April, 1960; CAS 77127, 250 mm SL, NE Pacific, off California, Oct. 1956; UW 20831, 166 mm SL, 58°33'N, 176°17'W, 10 Mar., 1981; UW 20832, 212 mm SL, 59°20'N, 178°09'W, 24 Feb., 1981; UW 22692, 90 mm SL, S of Chirinof I., 52°32'N, 155°35'W, 21 Jul. 1958; UW 22693, 101 mm SL, NE Pacific, 51°05'N, 176°25'W, 31 Jul. 1974; UW 22694, 217 mm SL, 56°33'N, 172°31'W, 13 Sep. 1980; UW 22695, 294 mm SL, 54°25'N, 166°33'W, 28 Feb. 1992; UW 22696, 317 mm SL, 54°39'N, 165°45'W, 27 Jun. 1989; UW 22697, 296 mm SL, 54°29'N, 166°11'W, 31 Jan. 1992; UW 22698, 239 mm SL, 54°10'N, 166°20'W, 11 Mar. 1990; UW 22699, 274 mm SL, 54°26'N, 166°16'W, 1992.

Allocyttus guineensis Trunov and Kukuev, in Trunov, 1982

Holotype.— not examined.

Paratypes (1 specimen).— ZIL 45503, 196 mm SL, SE Atlantic, 33°19'S, 02°20'E, 780 m, 6 Apr. 1977.

Other material.— none.

Allocyttus niger James, Inada and Nakamura, 1988

Holotype.— not examined

Paratypes.— not examined

Other material (21 specimens).—AMS I33319.001, 275 mm SL, off Ulladulla, 35°28'S, 150°52'E, 900 m, 1987; CSIRO H1378.03, 201 mm SL, W of Cape Sorell, 42°13'S, 144°39'E, 1080 m, 1988; CSIRO H1424.02, 210 mm SL, SW of Maatsuyker Island, 43°50'S, 145°52'E, 1130 m, 1988; CSIRO H1431.01, 197 mm SL, NW of Cape Sorell, 42°10'S, 144°37'E, 1055 m, 1988; CSIRO H2134.01, 192 mm SL, W of Trial Harbour, 41°59'S, 144°33'E, 1015 m, 1989; CSIRO H2135.01, 204 mm SL, WSW of Cape Sorell, 42°18'S, 144°43'E, 890 m, 1989; CSIRO H2333.01, 263 mm SL, CSIRO H2333.02, 255 mm SL, CSIRO H2333.03, 267 mm SL, CSIRO H2333.04, 235 mm SL, CSIRO H2333.05, 227 mm SL, CSIRO H2333.06, 222 mm SL, Maatsuyker Hill, 1990; CSIRO H2816.03, 223 mm SL, South Tasman Rise, 47°21'S, 148°47'E, 1100 m, 1992; CSIRO H2821.01, 207 mm SL, South Tasman Rise, 47°11'S, 148°48'E, 1180 m, 1992; CSIRO H3167.01, 193 mm SL, near Pedra Branca seamount, 44°15'S, 147°06'E, 700 m, 1992; CSIRO H3739.01, 209 mm SL, South Chatham Rise, 44°23'S, 175°41'E, 730 m, 1993; CSIRO H3743.01, 177 mm SL, Maatsuyker Hill area, 44°13'S, 146°11'E, 800 m, 1994; CSIRO H3972.02, 282 mm SL, Maatsuyker Hill area, 44°11'S, 146°09'E, 1050 m, 19 May 1995; CSIRO T349, 218 mm SL, SW of King Island, 40°37'S, 143°24'E, 935 m, 1983; CSIRO T703, 220 mm SL, SW of King Island, 40°35'S, 143°28'E, 940 m, 1983; CSIRO T709, 202 mm SL, SW of King Island, 40°34'S, 143°29'E, 510 m, 1983; QM I25473, Cascade Plateau, 43°59'S, 150°30'E.

Allocyttus verrucosus (Gilchrist, 1906)

Holotype.— not examined (probably lost).

Paratypes.— not examined.

Other material (163 specimens).— AMS I12888, AMS I12889, Great Australian Bight, 32°00'S, 129°18'E, 1913; AMS I18605-001 (2 specimens), 91 mm SL, 120 mm SL, E of South Africa, 24°22'S, 13°17'E, 570 m, 1968; AMS I18712-002 (4 specimens), 90–141 mm SL, AMS I18712-003, 220 mm SL, AMS I18712-004, 200 mm SL, AMS I18712-005, 220 mm SL, off S Australia, 33°46'S, 127°27'E, 1100 m, 1976; AMS I18726-009,

195 mm SL, AMS I18726-010, 230 mm SL, E of Broken Bay, 33°38'S, 151°57'E, 790 m, 1975; AMS I18839-039, 295 mm SL, E of Broken Bay, 33°25'S, 152°03'E 630 m, 1975; AMS I20068-001 (15 specimens), 88–118 mm SL, AMS I20068-031, (2 specimens), E of Broken Bay, 33°25'S, 152°11'E, 895 m, 1977; AMS I20098-001 (23 specimens), 175–255 mm SL, E of Broken Bay, 33°34'S, 152°01'E, 905 m, 1977; AMS I24058-002, 98 mm SL, off Kiama, 34°53'S, 151°14'E, 930 m, 1983; AMS 24462-001 (6 specimens), 88–127 mm SL, off Cape Hawke, 32°02'S, 153°09'E, 980 m, 1983; AMS I25590-001 (2 specimens), 150–195 mm SL, off Pieman River, 46°46'S, 145°26'E, 1984; AMS I28067-010 (3 specimens), 215–250 mm SL, off Broken Bay, 33°34'S, 158°08'E, 1979; AMS I28126-001 (2 specimens), 224–256 mm SL, NE of Maputo, 25°31'S, 35°25'E, 1230 m, 1988; AMS I 28139-005 (2 specimens), 95–175 mm SL, NW of Tulear, 22°29'S, 43°01'E, 960 m, 1988; AMS I29338-001, 225 mm SL, Lord Howe Rise, 28°05'S, 163°06'E, 1050 m, 1989; AMS I 30303-002 (2 specimens), 93–115 mm SL, E of Woy Woy, 33°29'S, 152°11'E, 970 m, 1989; AMS I30894-001 (2 specimens), 132–147 mm SL, Great Australian Bight, 34°25'S, 132°07'E, 1080 m, 1989; AMS I31150-006, 200 mm SL, off Northwest Cape, 21°51'S, 113°41'E, 1160 m, 1991; AMS I31157-002 (6 specimens), 111–185 mm SL, off Cape Cuvier, 23°58'S, 111°54'E, 1065 m, 1991; AMS I31181-008, 95 mm SL, SW of Shoal Point, 28°00'S, 112°41'E, 855 m, 1991; AMS I32491-002, 113 mm SL, Great Australian Bight; CAS 66564, 170 mm SL, Indian Ocean, off Madagascar, 3 Dec. 1988; CAS 66565, 226 mm SL, Indian Ocean, off Mozambique, 23 Nov. 1988; CSIRO H884.02, 265 mm SL; CSIRO H1201.05, 185 mm SL, Houtman Abrolhos, 29°05'S, 113°41'E, 880 m, 1988; CSIRO H1357.03, 90mm SL, E of St Marys, 41°35'S 148°43'E, 1008 m, 1986; CSIRO H1398.02, 101 mm SL, CSIRO H1398.03, 84 mm SL, W of Granville Harbour, 41°43'S, 144°24'E 970 m, 1988; CSIRO H1544.01, 92 mm SL, E of Brush Island, 35°24'S, 150°55'E, 930 m, 1988; CSIRO H1566.05, 235 mm SL, CSIRO H1566.06, 204 mm SL, S of King Island, 40°59'S, 143°42'E, 1255 m, 1985; CSIRO H2036.01, 192 mm SL, CSIRO H2306.02, 114 mm SL, Great Australian Bight, 34°16'S, 132°13'E, 820 m, 1989; CSIRO H2542.10, 136 mm SL, Exmouth Plateau, 20°07'S, 112°56'E, 855 m, 1991; CSIRO H2553.13, 98 mm SL, W of Point Cloates, 22°45'S, 113°13'E, 910 m, 1991; CSIRO H2559.04, 133 mm SL, CSIRO H2559.05, 147 mm SL, CSIRO H2559.06, 157 mm SL, CSIRO H2559.07, 180 mm SL, CSIRO H2559.08, 183 mm SL, W of Cape Cuvier, 23°58'S, 111°54'E, 1065 m, 1991; CSIRO H2626.02, 226 mm SL, CSIRO H2626.03, 206 mm SL, WSW of Point D'Entrecasteaux, 35°05'S, 114°58'E, 920 m, 1991; CSIRO H2977.01, 84 mm SL, Challenger Plateau , 37°34'S, 169°24'E, 1100 m, 1992; CSIRO H2985.03, 91 mm SL, Great Australian Bight, 33°50'S, 130°45'E, 995 m, 1992; CSIRO H3007.09 (6 specimens), SW of Albany, 35°26'S, 117°25'E 845 m, 1989; CSIRO H3010.08 (2 specimens), S of Cape Leeuwin, 35°07'S, 115°01'E, 945 m, 1989; CSIRO H3035.06, 164 mm SL, NW of Geraldton, 28°13'S, 113°07'E, 615 m SL, 1989; CSIRO H3282.01, 218 mm SL, CSIRO H3282.02, 204 mm SL, CSIRO H3282.03, 229 mm SL, CSIRO H3282.04, 215 mm SL, CSIRO H3282.05, 235 mm SL, CSIRO H3282.06, 254 mm SL, W of Tas., 1989; CSIRO H3590.01, 247 mm SL, CSIRO H3590.02, 166 mm SL, CSIRO H3590.03, 228 mm SL, CSIRO H3590.04, 272 mm SL, CSIRO H3590.05, 157 mm SL, SW of Port Elizabeth, 35°03'S, 24°06'E, 1005 m, 1993; CSIRO H3698.01, 101 mm SL, SW of Sandy Cape, 41°37'S, 144°21'E, 1095 m, 1988; CSIRO H3700.01 (3 specimens), 91–103 mm SL, Great Australian Bight, 33°32'S, 128°12'E, 990 m, 1989; CSIRO H3867.01, 145 mm SL, CSIRO H3867.02, 190 mm SL, South Chatham Rise, 44°35'S, 175°47'E, 1040 m, 1993; CSIRO T58, 148 mm SL, NW of Point Hibbs, 42°28'S, 144°44'E, 835 m, 1982; CSIRO T60, 273 mm SL, off Cape Grim, 40°42'S, 143°32'E, 1981; CSIRO T66, 252 mm SL, off Cape Grim, 40°42'S, 143°32'E, 1981; CSIRO T75, 226 mm SL, off Cape Grim, 40°42'S, 143°32'E, 1981; CSIRO T655.01, 125 mm SL, CSIRO T655.02, 116 mm SL, CSIRO T655.03, 108 mm SL, S of King Island, 40°59'S, 143°42'E, 1255 m, 1985; CSIRO T657, 246 mm SL, CSIRO T802, 274 mm SL, SW of Cape Martin, 37°48'S, 139°33'E, 960 m, 1983; CSIRO T1312, SW of King Island, 40°42'S, 143°29'E, 1060 m, 1982; CSIRO T1567 (11 specimens), 84–148 mm SL, Great Australian Bight, 33°43'S, 130°33'E, 1000 m, 1983; CSIRO T1908 (4 specimens), 290–297 mm SL, W of Sandy Cape, 41°20'S, 144°13'E, 1050 m, 1982; QM I1384, Great Australian Bight, 32°00'S, 129°28'E; SAM 32656, 180 mm SL, 29°38'S, 14° 25'E, 860 m 23 Jan. 1990; TMAG D146; WAM 73.001, 280 mm SL, Great Australian Bight, 31°43'S, 129°28'E, 14 May 1913; WAM 30216.003 (2 specimens), 211 mm SL, 227 mm SL, 27°32'S, 112°15'E, 2 Feb. 1991.

Allocyttus species (incertae sedis)

Other material (2 specimens).— CAS 58420, 78 mm SL, off Hawaii; CSIRO B1218, 230 mm SL, off Albany, Western Australia.

Neocyttus acanthorhynchus Regan, 1908

Holotype.— BMNH 1908.3.23.122, 99 mm SL, Saya de Malha Bank, NW of Madagascar, approximately 10'S, 60°E, 825 m, 1905.

Paratypes.— none.

Other material (1 specimen).— MNHN 1979-419, 152 mm SL, NE of Madagascar, 12°48'S, 048°03'E, 915m, Sep. 1972.

Neocyttus helgae (Holt and Byrne, 1908)

Holotype.— BMNH 1910.9.17.1, 193 mm SL, SW of Ireland, 51°36'N, 11°57'W, 1210 m, 3 Sep. 1907.

Paratypes.— none.

Other material (4 specimens).— CSIRO H3583.01, 262 mm SL, CSIRO H3583.02, 143 mm SL, CSIRO H3583.03, 241 mm SL, CSIRO H3583.04, 154 mm SL, W of the Faeroes, 61°39'N, 13°11'W, 1150 m, 19 Feb. 1993.

Neocyttus rhomboidalis Gilchrist, 1906

Holotype.— not examined.

Paratypes (2 specimens).— SAM 11973, 98 mm SL, BMNH 1904.5.28.14, 103 mm SL, off Cape Point, about 34°18'S, 18°22'E, 575–730 m, 16 Sep. 1903.

Other material (77 specimens).— AMS I12890, AMS I12891, AMS I12892, Great Australian Bight, 32°00'S, 129°18'E, 1913; AMS I17316-007 (3 specimens), 130–170 mm SL, off Sydney, 33°41'S, 152°56'E, 810 m, 1972; AMS I18726-001, 105 mm SL, AMS I18726-002, 165 mm SL, AMS I18726-003, 165 mm SL, AMS I18726-004, 150 mm SL, AMS I18726-005, 155 mm SL, AMS I18726-006, 145 mm SL, AMS I18726-007, 165 mm SL, AMS I18726-008, 160 mm SL, E of Broken Bay, 33°38'S, 151°57'E, 790 m, 1975; AMS I20099-001 (2 specimens), 90–98 mm SL, E of Broken Bay, 33°33'S, 152°02'E, 825 m, 1977; AMS I20099-015 (3 specimens), 153–175 mm SL, E of Broken Bay, 33°33'S, 152°02'E, 825 m, 1977; AMS I21812-002 (2 specimens), 67–84 mm SL, E of Sydney, 33°44'S, 151°57'E, 820 m, 1978; AMS I23885-002, 90 mm SL, E of Sydney, 34°53'S, 151°14'E, 830 m, 1978; AMS I24037-014 (2 specimens), 125–165 mm SL, E of Sydney, 33°47'S, 151°55'E, 850 m, 1978; AMS I25593-001, 200 mm SL, Great Australian Bight, 33°52'S, 131°01'E, 990 m, 1984; AMS I26245-005 (2 specimens), 108–128 mm SL, NE of Port Jackson, 33°44'S, 151°57'E, 1986; CSIRO C 4736, 232 mm SL, SW of Portland, 38°38'S, 141°03'E, 770 m, 1976; CSIRO H269.01, 227 mm SL, E of Maria Island, E Tasmania, 42°39'S, 148°25'E, 490 m, 15 Jul 1985; CSIRO H593.01, 326 mm SL, off Sandy Cape, W Tasmania, 41°S, 148°E, 495 m, 12 Jul. 1986; CSIRO H884.03, 260 mm SL; CSIRO H1566.07, 250 mm SL, S of King Island, 40°59'S, 143°42'E, 1000-1255 m, 1985; CSIRO H2034.01, 182 mm SL, CSIRO H2034.02, 189 mm SL, CSIRO H2034.03, 194 mm SL, NW of Cape Naturaliste, 33°03'S,

114°25'E, 700 m, 1989; CSIRO H2625.03, 144 mm SL, W of Point D'Entrecasteaux, 35°00'S, 114°42'E, 750 m, 1991; CSIRO H2626.04 , 159 mm SL, CSIRO H2626.05, 204 mm SL, WSW of Point D'Entrecasteaux, 35°05'S, 114°58'E, 920 m, 1991; CSIRO H2867.01, 171 mm SL, Great Australian Bight , 33°25'S, 129°55'E, 515 m, 1992; CSIRO H2873.01, 317 mm SL, CSIRO H2873.02, 272 mm SL, Great Australian Bight, 33°37'S, 129°54'E, 1100 m, 1992; CSIRO H3007.08, 95 mm SL, CSIRO H3007.12, 105 mm SL, H3007.13, 130 mm SL, CSIRO H3007.14, 139 mm SL, CSIRO H3007.15, 158 mm SL, SW of Albany, 35°26'S, 117°25'E, 845 m, 1989; CSIRO H3035.07, 85 mm SL, NW of Geraldton, 28°13'S, 113°07'E, 615 m, 1989; CSIRO H3282.08, 207 mm SL, CSIRO H3282.09, 285 mm SL, CSIRO H3282.10, 283 mm SL, CSIRO H3282.11, 309 mm SL, CSIRO H3282.12, 319 mm SL, W of Tas., 1989; CSIRO H3502.01, 270 mm SL, E of Maria Island, E Tasmania, 42°40'S, 148°25'E, 500 m, 24 Jul. 1993; CSIRO H3592.02, 222 mm SL, CSIRO H3592.03, 237 mm SL, SW of Point D'Entrecasteaux, 35°06'S, 115°31'E, 750 m, 1993; CSIRO H3741.01, 178 mm SL, South Chatham Rise, 44°33'S, 175°55'E, 775 m, 1993; CSIRO T68, 102 mm SL, CSIRO T71, 99 mm SL, NW of Point Hibbs, W Tasmania, 42°28'S, 144°44'E, 955 m, 24 Apr. 1985; CSIRO T76, 285 mm SL, Cascade Plateau, 43°52'S, 150°30'E, 1979; CSIRO T704, 333 mm SL, South Tasman Rise, SE of Tasmania, 43°52'S, 150°30'E, 850 m, 31 Dec. 1979; CSIRO T1313, SW of King Island, 40°42'S, 143°29'E, 1060 m, 1982; CSIRO T1419 (2 specimens), 89 mm SL, 109 mm SL, Great Australian Bight, 33°43'S, 130°33'E, 1000 m, 1983; CSIRO T1581.01, 115 mm SL, off Cape Sorell, W Tasmania, 42°S, 144°E, 580 m, Jan. 1979; CSIRO T1848.01, 290 mm SL, SW of King Island, NW Tasmania, 40°47'S, 143°32'E, 925 m, 16 Dec. 1981; IIPB 20/1981, 81 mm SL, IIPB 23/1981, 122 mm SL, IIPB 24/1981, 164 mm SL, off Namibia, 22°31'S, 12°47'E, 710 m, 11 Nov. 1979; QM I1385, Great Australian Bight, 32°00'S, 129°28'E; QM I23008, E of Terrigal, 33°27'S, 151°30'E; QM I 25356, New Zealand; SAM 27171, 76 mm SL, 28°21'S, 32°34'E, 825 m, 28 May 1975; SAM 23743, 228 mm mm SL, W of Cape Peninsula, Atlantic Ocean; TMAG D1628; TMAG D2020; WAM 70.001, 217 mm SL, Great Australian Bight, 31°43'S, 129°28'E, 14 May 1913; WAM 30500.001, 117 mm SL, 131 mm SL, 12 Jun. 1992.

Neocyttus sp. A

Holotype.— not designated.

Paratypes.— not designated.

Other material (25 specimens).— CSIRO H2865.01, 148 mm SL, CSIRO H2865.02, 172 mm SL, Pedra Branca seamount, S of Tasmania, 44°22'S, 147°08'E, 1170 m, 12 Feb. 1992; CSIRO H2864.01, 153 mm SL, CSIRO H2864.02, 157 mm SL, CSIRO H2864.03, 155 mm SL, CSIRO H2864.04, 144 mm SL, CSIRO H2864.05, 180 mm SL, CSIRO H2864.06, 152 mm SL, CSIRO H2864.07, 164 mm SL, CSIRO H2864.08, 169 mm SL, CSIRO H2864.09, 158 mm SL, CSIRO H2864.10, 147 mm SL, CSIRO H2864.11, 141 mm SL, CSIRO H2864.12, 124 mm SL, CSIRO H2864.13, 115 mm SL, Pedra Branca seamount, S of Tasmania, 44°23'S, 147°05'E, 1120 m, 11 Feb. 1992; CSIRO H3294.01, 184 mm SL, CSIRO H3294.02, 195 mm SL, CSIRO H3294.03, 163 mm SL, CSIRO H3294.04, 164 mm SL, CSIRO H3294.05, 146 mm SL, CSIRO H3593.01, 201 mm SL, Pedra Branca seamount, S of Tasmania, 44°14'S, 147°08'E, about 1100 m, between 15–19 May 1993; CSIRO H2823.05, 191 mm SL, South Tasman Rise, S of Tasmania, 47°30'S, 147°40'E, 1170 m, 14 Feb. 1992; CSIRO H2841.05, 153 mm SL, South Tasman Rise, S of Tasmania, 47°19'S, 148°46'E, 1120 m, 9 Jan. 1992; CSIRO H3591.01, 138 mm SL, South Tasman Rise, S of Tasmania, 47°12'S, 148°52'E, 1145 m, 6 Feb. 1992; CSIRO H3592.01, 166 mm SL, off Point D'Entrecasteaux, SW Western Australia, 35°06'S, 115°31'E, 750 m, 26 Aug. 1993.

Neocyttus sp. B

Holotype.— not designated.

Paratypes.— not designated.

Other material (1 specimen).— IOAN P15776, 131 mm SL, W of Sumatra, 3°46'S, 95°00'E, 875 m, 28 Feb. 1979.

Oreosoma atlanticum Cuvier, 1829

Holotype.— not examined.

Paratypes.— not examined.

Other material (52 specimens).— AMS I12878, AMS I12879, AMS I12880, AMS I12881, AMS I12882, AMS I12884, AMS I12885, 134 mm SL, AMS I12886, 149 mm SL, Great Australian Bight, 32°00'S, 129°18'E, 1913; AMS I17857-005, 120 mm SL, off Sydney, 33°47'S, 151°52'E, 675 m, 1972; AMS I19860-016, 127 mm SL, E of Broken Bay, 33°35'S, 152°01'E, 822 m, 1976; AMS I25933-013, 108 mm SL, off Broken Bay, 33°34'S, 152°08'E, 1979; AMS 20070-035, 32 mm SL, NE of Cape Howe, 37°24'S, 150°30'E, 3600 m, 1977; AMS I21370-003, 34 mm SL, off Newcastle, 32°55'S, 152°57'E, 1500 m, 1979; AMS I23885-001, 110 mm SL, E of Sydney, 34°53'S, 151°14'E, 830 m, 1978; AMS I25127, 136 mm SL, E of Shoalhaven Heads, 34°50'S, 151°15'E, 1984; AMS I25290, 120 mm SL, 33°45'S, 152°07'E, 1005 m, 1984; AMS I28165-006, 155 mm SL, Walters Shoals, 33°21'S, 44°05'E, 750 m, 1988; AMS I23885-011 (2 specimens), 100–105 mm SL, E of Sydney, 34°53'S, 151°14'E, 830 m, 1978; BMNH 1904.10.8.2, 102 mm SL, South Africa; SAM 23743 (3 specimens), 153 mm SL, 108 mm SL, 98 mm SL, W of Cape Peninsula, Atlantic Ocean; CSIRO A4277, 76 mm SL, E of Kiama, 34°38'S, 151°18'E, 1963; CSIRO A4278, 42 mm SL, E of Eddyston, 41'S, 148'E, 1954; CSIRO B1650, 31 mm SL, E of Bega, 36°39'S, 152°09'E, 45 m, 1978; CSIRO H884.01, 164 mm SL; CSIRO H973.02, 41 mm SL, off St Patrick's Head; CSIRO H1384.01, 106 mm SL, W of Cape Sorell, 42°17'S, 144°42'E, 965 m, 1988; CSIRO H1394.01, 105 mm SL, W of Granville Harbour, 41°51'S, 144°27'E, 935 m, 1988; CSIRO H1398.01, 99 mm SL, W of Granville Harbour, 41°43'S, 144°24'E, 970 m, 1988; CSIRO H2228.02, 134 mm SL, Great Australian Bight, 34°03'S, 131°36'E, 1120 m, 1989; CSIRO H2514.01, 81 mm SL, S of Maatsuyker Island, 44°13'S, 146°11'E, 1260 m, 1990; CSIRO H2699.01, 44 mm SL, St Helens Hill, 41°14'S, 148°45'E, 1000 m, 1991; CSIRO H2863.01, 133 mm SL, CSIRO H2863.02, 124 mm SL, Pedra Branca Area, 44°11'S, 147°13'E, 950 m, 1992; CSIRO H3016.01, 133 mm SL, CSIRO H3016.04, 146 mm SL, CSIRO H3016.05, 147 mm SL, SW of Busselton, 34°15'S, 114°20'E, 825 m, 1989; CSIRO H3262.01, 46 mm SL, E of Scamander, 41°30'S, 149°09'E, 1992; CSIRO H3699.01, 79 mm SL, Pedra Branca Area, 44°10'S, 147°11'E, 1090 m, 1992; CSIRO H3701.01, 48 mm SL, off S Tasmania,1990; CSIRO T1908.03, 110 mm SL, W of Sandy Cape, 41°20'S, 144°13'E, 1050 m, 1982; SAM 27868 (2 specimens), 115 mm SL, 115 mm SL, 30°32'S, 30°52'E, 900 m, 10 May 1977; QM I1386, QM I1387, QM I1388, Great Australian Bight, 32°00'S, 129°28'E; WAM 75.001 (3 specimens), Great Australian Bight, 31°43'S, 129°28'E; TMAG D1629.

Pseudocyttus maculatus Gilchrist, 1906

Holotype.— lost.

Paratypes.— none designated.

Other material (33 specimens).— AMS I20098-014, 195 mm SL, E of Broken Bay, 33°34'S, 152°01'E, 905 m, 1977; AMS I21203-003, 160 mm SL, S of Tasmania, 47°15'S, 148°31'E, 950 m, 1975; AMS I24056-006,

156 mm SL, off Broken Bay, 33°38'S, 151°03'E, 895 m, 1983; AMS I24060-014 (2 specimens), 169–172 mm SL, 33°48'S, 151°57'E, 960 m, 1983; AMS I24424-004, 315 mm SL, off Brush Island, 35°30'S, 150°52'E, 1060 m, 1983; AMS I24447-002, 170 mm SL, off Norah Head, 33°28'S, 152°14'E, 1005 m, 1983; AMS I25463-001, 192 mm SL, off Pieman River, 1984; AMS I25651-002, 162 mm SL, off Pieman River, 41°46'S, 145°26'E, 1984; CSIRO H1293.03, 365 mm SL, NW of Macquarie Harbour, 41°47'S, 144°22'E, 1230 m, 1987; CSIRO H1566.34, 158 mm SL, S of King Island, 40°59'S, 143°42'E, 1255 m, 1985; CSIRO H2702.01, 179 mm SL, NE of Flinders Island, 39°16'S, 148°49'E, 1000 m, 1991; CSIRO H2711.01, 340 mm SL, Pedra Branca seamount, 44°16'S, 147°04'E, 850 m, 1991; CSIRO H2819.03, 129 mm SL, South Tasman Rise, 1020 m, 1992; CSIRO H3008.01, 209 mm SL, CSIRO H3008.14, 180 mm SL, SW of Albany, 35°25'S, 117°21'E, 840 m, 1989; CSIRO H3261.01, 510 mm SL, CSIRO H3261.02, 540 mm SL, Lord Howe Rise, 1992; CSIRO H3282.07, 157 mm SL, W of Tas., 1989; CSIRO H3742.01, 220 mm SL, South Chatham Rise, 44°29'S, 177°37'E, 815 m, 1993; CSIRO H3972.01, 390 mm SL, Maatsuyker Hill area, 44°11'S, 146°09'E, 1050 m, 19 May 1995; CSIRO T741, 151 mm SL, CSIRO T794, 169 mm SL, E of Seymour, 41°46'S, 148°37'E, 850 m, 1982; CSIRO T754, 151 mm SL, SW of King Island, 40°26'S, 143°19'E, 940 m, 1983; CSIRO T1273 (2 specimens), 145 mm SL, 149 mm SL, Tas?, 930 m; SAM 23802, 304 mm SL, W of Cape Town, Atlantic Ocean, 550 m, 4 Nov. 1963; SAM 23808, 158 mm SL, SW of Cape Columbine, 695 m, 11 Nov. 1963; QM I21279, New Zealand; QM I25472, Cascade Plateau, 43°59'S, 150°30'E; QM I27248, South Australia; TMAG D1420; TMAG D1765.

5.1.2. FROZEN SPECIMENS (FOR PHYLOGENY AND STOCK STRUCTURE ANALYSES)

Whole fish were frozen after capture and transported frozen to the laboratory. In the laboratory fish were thawed, labelled, measured (standard length) and sexed, samples of muscle and liver tissue were dissected, and the pyloric caecae were removed for counting. The tissue samples were stored at -80°C until analysed. The whole fish were refrozen for later meristic (and in the case of *N. rhomboidalis*, morphometric) analysis.

Sample details are given in Tables 5.1 - 5.5.

5.2. MERISTIC EXAMINATION

Meristic data were collected for two purposes: species diagnoses (taxonomic comparisons of all oreosomatids) and stock delineation of *Allocyttus niger* (black oreo), *Allocyttus verrucosus* (warty oreo), *Neocyttus rhomboidalis* (spikey oreo) and *Pseudocyttus maculatus* (smooth oreo).

5.2.1. MERISTIC EXAMINATION: TAXONOMIC COMPARISONS

Methods follow Hubbs and Lagler (1958) except where noted. The following counts were taken from specimens of all oreosomatid species:

> dorsal-fin spines (DS); dorsal-fin soft rays (DR); combined dorsal-fin spines and soft-rays (CD); anal-fin spines (AS); anal-fin soft rays (AR); combined anal-fin spines and soft rays (CA); left pelvic-fin spines (LVS); left pelvic-fin soft-rays (LVR); left pectoral-fin rays (LP); left upper gill-rakers (LUGR); left lower gill-rakers (LLGR); lateral line count (LL); pyloric caeca (PC); and total vertebrae (TV). Caudal fin counts are divided into the following components: dorsal

procurrent rays, dorsal unbranched rays, branched rays, ventral unbranched rays, and ventral procurrent rays.

Data were taken from the following specimens (those marked with a (V) were radiographed to take vertebral counts):

Allocyttus folletti—UW 20831 (V), UW 20832 (V), UW 22694 (V), UW 22695 (V), UW 22696, UW 22697 (V), UW 22698 (V), UW 22699 (V).
Allocyttus guineensis—ZIL 45501 (V only), ZIL 45501A (V only), ZIL 45502 (V only), ZIL 45503 (V).
Allocyttus niger—CSIRO H1424.02, CSIRO H1431.01, CSIRO H2134.01, CSIRO H2135.01, CSIRO H2333.01 (V), CSIRO H2333.02 (V), CSIRO H2333.03 (V), CSIRO H2333.04 (V), CSIRO H2333.05 (V), CSIRO H2816.03 (V), CSIRO H2821.01 (V), CSIRO T349 (V), CSIRO T703 (V), CSIRO T709.
Allocyttus verrucosus—CSIRO H1201.05, CSIRO H1544.01 (V), CSIRO H1566.05 (V), CSIRO H1566.06 (V), CSIRO H2036.01, CSIRO H2626.03 (V), CSIRO H2985.03, CSIRO H3035.06, CSIRO T58, CSIRO T66 (V), CSIRO T75, CSIRO T657 (V), CSIRO T802, CSIRO T1567 (3 specimens, V).
***Allocyttus* sp.**—CAS 58420.
Neocyttus acanthorhynchus—BMNH 1908.3.23.122 (V), MNHN 1979-419.
Neocyttus helgae—BMNH 1910.9.17.1 (V), CSIRO H3583.01 (V), CSIRO H3583.02 (V), CSIRO H3583.03 (V), CSIRO H3583.04 (V).
Neocyttus rhomboidalis—CSIRO H593.01 (V), CSIRO H2034.03 (V), CSIRO H3007.08 (V), CSIRO H3007.12 (V), CSIRO H3007.13 (V), CSIRO H3007.14 (V), CSIRO H3007.15 (V), CSIRO H3282.10 (V), CSIRO H3282.12 (V), CSIRO T1419 (2 specimens, V).
***Neocyttus* sp. A**—CSIRO H2865.01 (V), CSIRO H2865.02 (V), CSIRO H2864.01 (V), CSIRO H2864.03 (V), CSIRO H2864.04 (V), CSIRO H2864.05 (V), CSIRO H2864.06 (V), CSIRO H2864.07 (V), CSIRO H2864.08 (V), CSIRO H2864.09 (V), CSIRO H2864.10 (V), CSIRO H2864.11 (V), CSIRO H2864.12 (V), CSIRO H2864.13 (V), CSIRO H3294.03 (V), CSIRO H3593.01 (V).
***Neocyttus* sp B**—IOAN P15776.
Oreosoma atlanticum—CSIRO H884.01 (V), CSIRO H2514.01 (V), CSIRO H2699.01 (V), CSIRO H2863.01 (V), CSIRO H3016.01 (V), CSIRO H3016.04 (V), CSIRO H3016.05 (V).
Pseudocyttus maculatus—CSIRO H1293.03 (V), CSIRO H1566.34 (V), CSIRO H2702.01 (V), CSIRO H3008.01 (V), CSIRO H3008.14 (V).

5.2.2. MERISTIC EXAMINATION: STOCK STRUCTURE ANALYSES

Meristic counts were made on individuals from all suitable (i.e. undamaged) samples of the four main commercial species (black, smooth, warty, and spikey oreos). Counts were taken as above (for species diagnoses) with the following exceptions:

> left middle gill rakers (LMGR) are the gill raker(s) in the angle of the first left gill arch; right middle gill rakers (RMGR) are the gill raker(s) in the angle of the first right gill arch; lateral line (LL) is the entire series of lateral line scales; paired fins and gill rakers were counted on both sides of each fish.

The ventral fin characters showed insufficient variation for statistical analysis and are not considered further. The following groups of characters were combined for further analysis DS + DR = CD, AS + AR = CA, LUGR + LMGR + LLGR = LTGR, and RUGR + RMGR + RLGR = RTGR.

Differences between samples for each species were analysed by the randomised Monte Carlo chi-square procedure of Roff and Bentzen (1989), as described in section

5.4.3. Likewise, when multiple tests were carried out, the standard Bonferroni procedure (Lessios, 1992) was applied.

Asymmetry was examined by comparing the number of left and right pectoral fin rays (LP and RP) and the total number of left and right gill rakers (LTGR and RTGR). Both paired t-tests and Wilcoxon signed rank tests (nonparametric) were used to examine asymmetry, the former results are presented here. Lateral line counts and pyloric caeca counts were compared between samples through ANOVAs.

5.3. MORPHOMETRIC EXAMINATION

Morphological data were collected for two purposes: species diagnoses (taxonomic comparisons of all oreosomatids) and stock delineation of *Neocyttus rhomboidalis* (spikey oreos).

The reason for the latter was that genetic data (see section 7.5) revealed the presence of distinct genetic groups of spikey oreo, related to depth. These groups were distinguished by *sSOD** allele frequencies, samples with a high frequency of *sSOD*140* (>0.60) being found in deeper water (>700m) and samples with a low frequency of *sSOD*140* (<0.25) in shallower water (<700m). We were interested to see whether these two groups of spikey oreo differed in body shape.

5.3.1. MORPHOMETRIC EXAMINATION: TAXONOMIC COMPARISONS

Following the methods of Hubbs and Lagler (1958) (except where noted), the measurements below were taken (using vernier calipers) from specimens of all oreosomatid species:

> standard length (SL, from between lachrymal tips anteriorly); body depth (BD, direct from dorsal-fin origin to anal-fin origin); head length (HL, direct from between lachrymal tips to posterior margin of operculum, excluding opercular membrane); head width (HW, maximum width, posterior to eye); orbit diameter (OD); predorsal length (PDL, direct from between lachrymal tips to dorsal-fin origin); first dorsal-fin spine height (1DSH, direct from insertion to spine tip); second dorsal-fin spine height (2DSH, direct from insertion to tip); second dorsal-fin spine length (2DSL, maximum length); pelvic–anal interspace (VAO, distance from pelvic-fin insertion to anal-fin origin).

In addition, lachrymal width (LW, minimum width ventral to anterior of eye) was measured for all *Allocyttus* and *Neocyttus* specimens.

Morphometric data were taken from the following specimens:

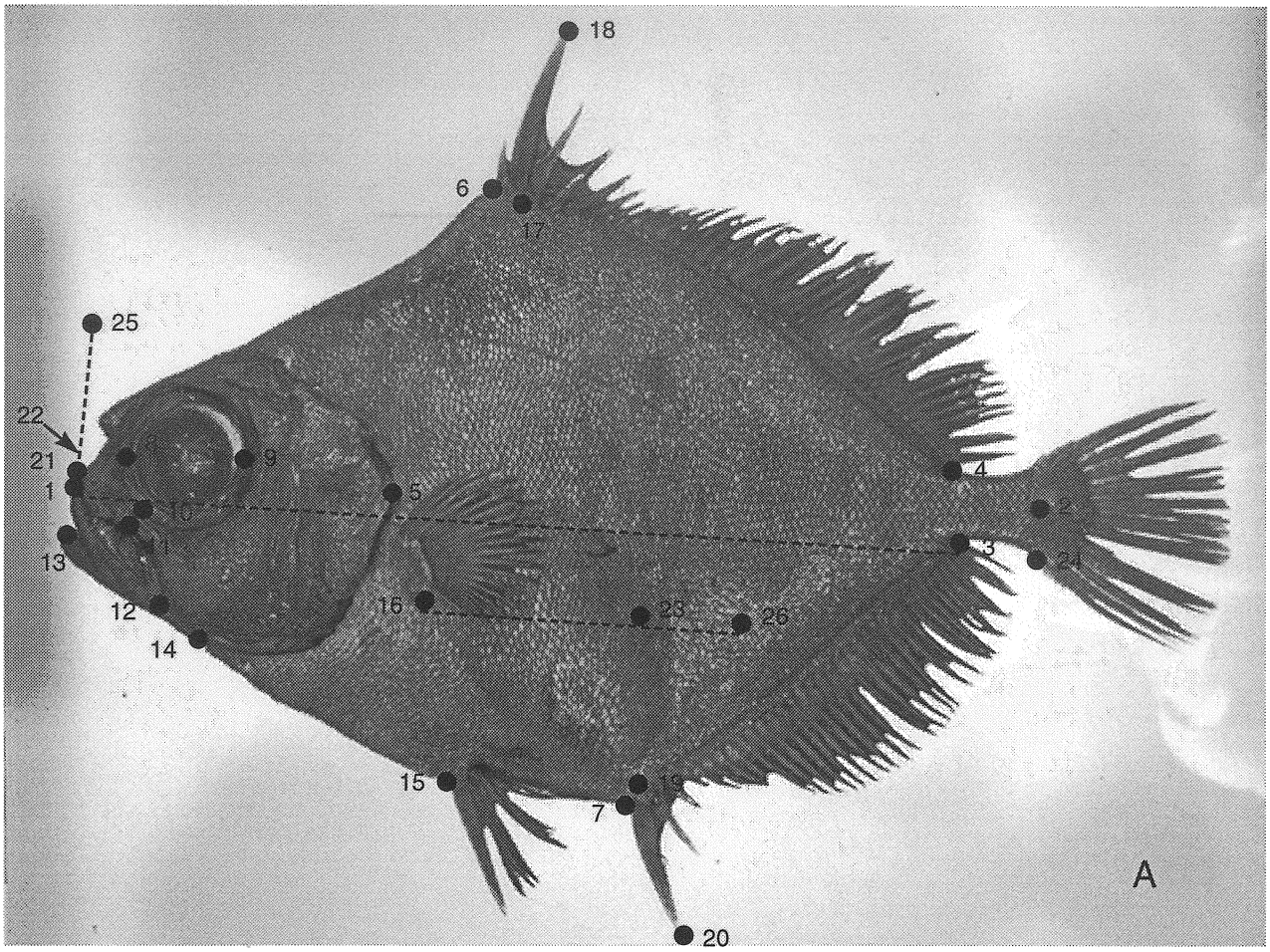
Allocyttus folletti—ADULTS: CAS 26784, CAS 77127, UW 20831, UW 20832, UW 22694, UW 22695, UW 22696, UW 22697, UW 22698, UW 22699. LARGE JUVENILES: UW 22693.
Allocyttus guineensis—ADULTS: ZIL 45503.
Allocyttus niger—ADULTS: CSIRO H2333.01, CSIRO H2333.02, CSIRO H2333.03, CSIRO H2333.04, CSIRO H2333.05, CSIRO H2333.06, CSIRO H3739.01, CSIRO H3972.02. LARGE JUVENILES: CSIRO H1431.01, CSIRO H2134.01, CSIRO H3167.01, CSIRO T349, CSIRO T709.
Allocyttus verrucosus—ADULTS: CSIRO H2626.02, CSIRO H2626.03, CSIRO H3282.01, CSIRO H3282.02, CSIRO H3282.03, CSIRO H3282.05, CSIRO H3282.06, CSIRO T66, CSIRO T75, CSIRO T802. LARGE JUVENILES: CSIRO H1544.01, CSIRO H2977.01, CSIRO T1567 (5 specimens), CSIRO T1908.04.
***Allocyttus* sp.**—LARGE JUVENILES: CAS 58420.
Neocyttus acanthorhynchus—ADULTS: BMNH 1908.3.23.122, MNHN 1979-419.
Neocyttus helgae—ADULTS: BMNH 1910.9.17.1, CSIRO H3583.01, CSIRO H3583.02, CSIRO H3583.03, CSIRO H3583.04.
Neocyttus rhomboidalis—ADULTS: CSIRO H269.01, CSIRO H593.01, CSIRO H1566.07, CSIRO H3282.09, CSIRO H3282.10, CSIRO H3502.02, CSIRO H3592.03, CSIRO H3741.01, CSIRO T68, CSIRO T704, CSIRO T1848.01. LARGE JUVENILES: CSIRO H3007.08, CSIRO H3007.12, CSIRO H3035.07, CSIRO T71, CSIRO T1581.01.
***Neocyttus* sp. A**—ADULTS: CSIRO H2865.01, CSIRO H2865.02, CSIRO H2864.01, CSIRO H2864.03, CSIRO H2864.04, CSIRO H2864.05, CSIRO H2864.06, CSIRO H2864.07, CSIRO H2864.08, CSIRO H2864.09, CSIRO H2864.10, CSIRO H2864.11, CSIRO H2864.12, CSIRO H2864.13, CSIRO H3294.03, CSIRO H3593.01.
***Neocyttus* sp. B**—IOAN P15776.
Oreosoma atlanticum—ADULTS: CSIRO H884.01, CSIRO H1384.01, CSIRO H1394.01, CSIRO H1398.01, CSIRO H2863.01, CSIRO H2863.02, CSIRO H3016.01, CSIRO H3016.04, CSIRO H3016.05. SMALL JUVENILES: CSIRO A4278, CSIRO B1650, CSIRO H973.02, CSIRO H2514.01, CSIRO H2699.01, CSIRO H3262.01, CSIRO H3699.01, CSIRO H3701.01.
Pseudocyttus maculatus—ADULTS: CSIRO H1293.03, CSIRO H2711.01, CSIRO H3972.01. LARGE JUVENILES: CSIRO H1566.34, CSIRO H2702.01, CSIRO H3008.01, CSIRO H3742.01, CSIRO T794.

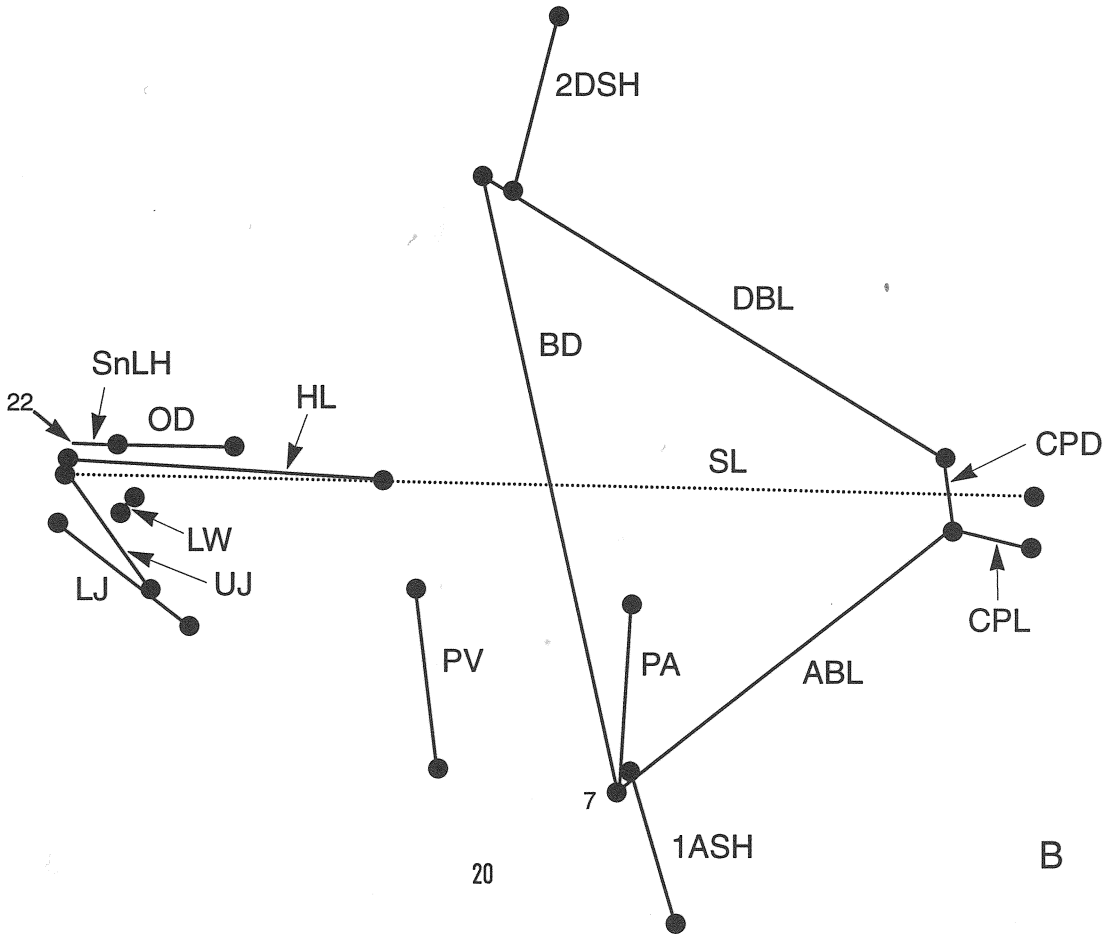
5.3.2. MORPHOMETRIC EXAMINATION: STOCK DELINEATION OF SPIKEY OREOS

Computer image analysis was used for the morphometric analysis. The system software was MorphoSys version 1.29 and the hardware a 386 PC with a PC frame grabber attached to a high resolution camera. The fish was placed on a white foam background beneath the camera and black and white pins used to mark morphometric landmarks on and around the fish. Twenty six points were defined to construct the truss used for measuring point-to-point distances (Table 5.6, Figure 5.1). These points were labelled with pins selected to contrast with their background, and give high precision of marking a point for morphometric analysis. A line through points 1 and 3 was taken as the horizontal axis of each specimen. The focus of the camera was altered so that each fish filled the entire frame. Scaling was set using a 100mm rule in a cross-haired fashion on white perspex.

Each frame in MorphoSys was constructed by sequentially marking landmark features with numbered points. The coordinates of these points and scaling factors were saved to a frame file. A measurement command file was applied to the frame. The command file was programmed to create four more essential points (Table 5.6, Figure 5.1), and to measure distances between specified points. Measurements follow those above (for

Figure 5.1. Points marked (A) and measurements taken (B) in the morphometric analysis of *Neocyttus rhomboidalis* using MorphoSys.





species diagnoses) except for HW, PDL, 1DSH, 2DSL and VAO, and with the following additions and changes:

> head length (HL, horizontal); snout length (SnLH, horizontal); upper jaw length (UJ); lower jaw length (LJ); dorsal-fin base length (DBL); anal-fin base length (ABL); pectoral–pelvic distance (PV, direct distance between pectoral-fin insertion and pelvic-fin origin); pectoral–anal distance (PA); vertical distance between pectoral-fin base and anal-fin origin); first anal-fin spine height (1ASH); caudal peduncle depth (CPD); caudal peduncle length (CPL); interorbital width (IOW).

The measurements are listed in Table 5.7 (see also Figure 5.1). Measurements were also expressed as a proportion of standard length. Interorbital width was measured using vernier calipers.

Fish used for morphometric analysis were a subset of the fish used for meristic analysis. An attempt was made to examine ten fish of each of the three *sSOD** genotypes per population, but the gene distributions were such that in each population one or more genotypes were at low frequency, and sample sizes were sometimes low. Thus all but one sample (South Australia) had less than ten of one or two genotypes (Table 7.32).

Anal-fin spine length, dorsal-fin spine length, and interorbital width were found to be unreliable variables and were excluded from further analysis. Approximately half of the fish measured had fin spines broken at varying lengths from the body, and interorbital width was affected by damage to the head area which was common amongst the specimens.

Measurement data were checked in the statistical package Systat 5.1 for non-uniform growth of the different measurement variables. A model was fitted that took into account both genotype and stock. Because some sample sizes of genotype within stocks were small, a new factor was created called stockgeno; Stockgeno=Stock*10+Genotype.

To check that the same standardisation model was appropriate for all stockgeno groups, the model ln(variable) = ln(standard length) + Stockgeno + Stockgeno*ln(standard length) was fitted to each group. The interaction term Stockgeno*ln(standard length) was checked for significance. Where Stockgeno*ln(standard length) was not significant, it was assumed that the regression lines were parallel, and the same standardisation model could be used for all groups. Residual plots were also checked to confirm validity of the statistical tests.

Fish shorter than 200 mm standard length did not fit the growth equation. Most of the New Zealand fish were smaller than 200 mm, and consequently the New Zealand sample was excluded from further analysis.

The allometric growth equation $M_{std,i} = M_i * \left(\frac{SL_{std}}{SL_i}\right)^{\beta}$ was used to standardise

measurement data. SL_{std} is a standardising constant, SL_i is the observed standard length for each fish, M_i is the observed measurement and $M_{std,i}$ is the standardised measurement. β is a growth constant that standardises each measurement variable as a proportion of standard length over the range of possible standard lengths. A value for β was obtained by fitting the model ln(variable)=constant+ln(standard length)+genotype to each variable. β was obtained from the regression coefficient for the ln(standard length) term in the model.

Anovas and Manovas were done to check for significant interactions between stock and the two homozygous *sSOD** genotypes. Bass Strait and West Tasmania were excluded from this analysis as they lacked specimens of one particular homozygote. All stocks were included to examine the main effects of genotype and stock; this was possible as there was no interaction term included in the model.

Canonical variant analyses were used to investigate stock separation. These analyses included all fish (i.e. all three genotypes) that were analysed morphometrically.

5.4. GENETIC EXAMINATION

5.4.1. GENETIC EXAMINATION: ALLOZYME ELECTROPHORESIS

Small pieces of white muscle or liver tissue (Table 5.8) were placed in 1.5 mL microcentrifuge tubes, homogenised manually with a few drops of distilled water, and spun at 11 000 g in a microcentrifuge for 2 minutes. The supernatant was used for electrophoresis.

Allozyme variation was examined with three gel systems: gel system A – Helena Titan III cellulose acetate plates run at 200 V with a Tris-glycine buffer system (0.02 M tris and 0.192 M glycine; Hebert and Beaton, 1989); gel system B – Helena Titan III cellulose acetate plates run at 150 V with a Tris-citrate buffer system (0.075 M tris and 0.025 M citric acid, pH 7.0); gel system C – starch gels (8% Connaught) run with a discontinuous histidine–citrate buffer system (gel buffer 0.005M histidine HCl pH 7.0; electrode buffer 0.41M trisodium citrate pH 7.0). Staining techniques were largely as in Hebert and Beaton (1989).

In all, 19 enzymes, representing 28 loci, were examined (Table 5.8). However, the loci *GPI–A** and *sMEP** were not included in some of the analyses because of poor resolution in some species. Loci and alleles were designated by the nomenclature system outlined in Shaklee *et al.* (1990), except that peptidase loci were identified as *PEP1** and *PEP2**. Multiple loci encoding the same enzyme were designated by consecutive numbers, with '1' denoting the fastest migrating system. Alleles within each locus were numbered according to the anodal mobility (rounded to nearest 5%, except *FH*113*) of their product relative to that of the most common allele observed in the spikey oreo *N. rhomboidalis*, which was designated '100' (cathodal migration was designated negative). In order to simplify some tables, alleles were also designated

alphabetically, with 'a' denoting the fastest migrating allele product observed in the ten species. In addition muscle protein patterns were examined after Coomassie Blue staining. These results are not included in the phylogenetic analyses (section 6.3) because of uncertain homologies between species, but patterns were species-specific and protein loci were included in assessments of genetic diversity within species (Chapter 7). All protein loci were found to be monomorphic within species, but since homologies with the spikey oreo are uncertain, alleles are designated as "x" within each species rather than being attributed relative mobility designations.

5.4.2. GENETIC EXAMINATION: MITOCHONDRIAL DNA PROCEDURES

Total DNA was extracted from approximately 100 mg of white muscle tissue per individual by a modified CTAB (hexadecyltrimethylammoniumbromide) protocol described by Grewe *et al.* (1993). In an initial survey, DNA was digested by 17 restriction enzymes and then the ten enzymes showing the best resolution of fragment patterns were selected for each species (Table 5.9). Restriction fragments were separated in horizontal 1.0% agarose gels submerged in a tris-borate-EDTA (TBE) buffer system (Sambrook *et al.,* 1989). DNA was transferred to a nylon membrane filter (Hybond N+, Amersham Ltd.) by southern blotting transfer (Sambrook *et al.,* 1989). The nylon membrane filters were probed with blue eye trevalla (*Hyperoglyphe antarctica*, Teleostei: Stromateoidei) mitochondrial DNA (50 ng used per ten 20 cm x 20 cm blots) purified by caesium chloride (CsCl) ultracentrifugation. The trevalla probe was labelled with 32P dCTP (Bresatec Pty Ltd), using a GIGAprime DNA labelling kit (Bresatec Pty Ltd). The membrane filters were then exposed to Kodak XAR-5 X-ray film for 48-72 h, at -20°C.

Restriction enzyme digestion profiles were given letter designations, in order of discovery. Restriction fragments were sized with the assistance of the program DNAGEL (Keiser 1984).

PCR analysis of Spikey oreo samples:

PCR (polymerase chain reaction) amplification of the ND5/6 fragment of the mitochondrial genome of spikey oreo *N. rhomboidalis*, followed by restriction digestion with the enzymes *Hin* PI and *Sty* I, was used to further investigate the observed allozyme (*sSOD**) differentiation between 'deep' and 'shallow' caught samples.

The selection of this region of the mtDNA genome and the restriction enzymes followed trials with eleven primer pairs (Bresatec Pty. Ltd.) and thirteen restriction enzymes; final selection was based on reliability of amplification, clarity and polymorphism shown. The primer pair for the ND5/6 fragment was C.Leu3-L/CB2-H. Sequences of the primers are: C.Leu3-L, 5'GGA ACC AAA AAC TCT TGG TGC AAC TCC (Park *et al.*, 1993), and CB2-H, 5'CCC TCA GAA TGA TAT TTG TCC TCA (Kocher *et al., 1989*).

Each PCR reaction was made up in a 50 µl volume, consisting of: 2 µl of each primer (@ 10 µM concentration), 4 µl each dNTP, 20 µl template DNA (@ 10 ng/µl), 0.5 units *Taq* polymerase, 5 µl buffer solution and 17 µl double distilled water. The PCR conditions (Perkin Elmer 9600 thermal cycler) applied were: 1 cycle: denaturation @ 94°C for 5 minutes; annealing @ 55°C for 30 seconds; extension @ 72°C for 2 minutes; then 40 cycles: 94°C for 30s; 50°C for 30s 72°C for 2 minutes.; final extension @ 72°C for 10 minutes, followed by holding @ 4°C. Sufficient amplification of the PCR product was tested by DNA flourometry.

Restriction fragments were separated in horizontal 1.2% agarose gels containing ethidium bromide and submerged in a tris-borate-EDTA (TBE) buffer system (Sambrook *et al.,* 1989). All gels were run @ 25 volts overnight and resulting fragments were visualised under UV light and photographed.

5.4.3. GENETIC EXAMINATION: STATISTICAL ANALYSES

Deviations from expected Hardy–Weinberg genotype proportions were tested by chi-square tests with BIOSYS-1 (Swofford and Selander, 1981). Valid tests were considered to be those with a minimum expected number per genotype of 1 or greater. In order to achieve this, rare alleles were pooled, but extreme allele frequencies and small sample sizes precluded statistically valid tests in some instances. Levene's (1949) correction for small sample sizes was used.

Heterogeneity across the samples, for both allele and mtDNA haplotype frequencies, was tested by the randomised Monte Carlo chi-square procedure of Roff and Bentzen (1989), which obviates the need to pool rare alleles. For each test, 1000 randomisations of the data were carried out, each producing a randomised chi-square value (χ^2null). The probability that the null hypothesis of genetic homogeneity was valid was given by P = n/1000, where n is the number of randomisations that generate χ^2null values greater than or equal to the chi-square value given by the actual data.

Differentiation among samples was quantified using Nei's gene diversity statistic G_{ST} (Nei, 1973), which reflects the proportion of total genetic variation attributable to differentiation between samples. G_{ST} was estimated for each locus by $(H_T - H_S)/H_T$, where H_T represents the total heterozygosity (or haplotype diversity) and H_S the average (Hardy–Weinberg expected) population heterozygosity. The proportion or magnitude of G_{ST} generated by sampling error, termed $G_{ST\ .null}$, was estimated using a bootstrapping program, given the observed allele or haplotype frequencies and sample sizes (Elliott and Ward, 1992). Simulations were run 1000 times to provide a mean value of $G_{ST\ .null}$ and a standard deviation. The probability of obtaining a mean value of $G_{ST\ .null}$ as large as or larger than that obtained from the actual observations, G_{ST}, was given by P = n/1000, where n is the number of randomisations that generated $G_{ST\ .null} \geq G_{ST}$. Values of $P < 0.05$ indicated significant differentiation between samples that could not be explained by sampling error alone.

When multiple tests were carried out, the standard Bonferroni procedure (Lessios, 1992) was applied. The predetermined significance level of 0.05 was adjusted according to the number of tests performed.

Haplotype (nucleon) and nucleotide diversity within samples were computed with the REAP package (McElroy *et al.,* 1992), using the formulations of Nei and Tajima (1981) and Nei (1987). Note that because of uncertainties with determining cut site homologies with *Sty* I, data from this enzyme were not used in estimating nucleotide diversities but were used for determining haplotype diversities.

Species relationships were analysed with BIOSYS-1 (Swofford and Selander, 1981) and PAUP 3.0s (Phylogenetic Analysis using Parsimony; Swofford, 1991). Two phenetic methods of analysis of genetic distance obtained from the allele frequency data were examined with BIOSYS-1: Nei's (1978) unbiased genetic distance measure with cluster analysis and the unweighted pair-group method with arithmetic averaging (UPGMA) (a method also used to estimate relationships among spikey oreo samples), and Rogers (1972) distance measure with the distance-Wagner procedure (Farris, 1972) and outgroup rooting. The Wagner procedure, unlike the UPGMA analysis, does not assume a constant rate of evolution. For the cladistic maximum-parsimony analysis (PAUP), the loci were coded as characters and the most common alleles as unordered character states. When two common alleles were at equal frequencies they were treated as multiple states and interpreted in the analysis as a polymorphism. The "branch and bound" and "exhaustive" routines were applied to search for the most parsimonious tree.

Table 5.1. Black oreo. Sample details. N = the number of individuals collected and may include both juvenile fish or fish that were not sexed. Size (standard length, except NZ total length) is presented as the mean ± standard deviation and range in brackets.

Sample and Abbreviation	Location	Depth (m)	Date	N	Sex	Size (mm)
Western Australia WA	?34° 45' S 114° 16' E	850	October 1993	10	Female - 4 Male - 6	297 ± 40 (215-333)
Southern Tasmania STAS	44° 13' S 146° 11' E	915	May 1993	202	Female - 133 Male - 59	318 ± 30 (236-395)
South Tasman Rise STR	47° 12' S 148° 48' E	880 to 1195	January & May 1992	44	Female - 26 Male - 13	285 ± 38 (220-350)
New Zealand NZ	44° 50' S 176° E	950	January 1994	99	Female - 49 Male - 42	293 ± 44 (242-383)

Table 5.2. Smooth oreo. Sample details. N = the number of individuals collected and may include both juvenile fish or fish that were not sexed. Size (standard length, except NZ total length) is presented as the mean ± standard deviation and range in brackets.

Sample and Abbreviation	Location	Depth (m)	Date	N	Sex	Size (mm)
Western Australia WA	34° 45' S 114° 16' E	850	October 1993	99	Female - 48 Male - 49	413 ± 49 (208-530)
Western Tasmania WTAS	41° 50' S 144° 30' E	600	August 1992	8	Female - 1 Male - 1	267 ± 68 (155-380)
Southern Tasmania STAS	44° 14' S 147° 08' E	900 to 1300	May 1993	200	Female - 140 Male - 58	329 ± 39 (162-425)
South Tasman Rise STR	47° 10' to 47° 40' S 147° 40' to 148° 50' E	880 to 1195	January/ February 1992	67	Female - 35 Male - 9	241 ± 70 (128-398)
Lord Howe Rise LHR	36° S 165° 30' E	800 to 1000	August 1993	15	Female -13 Male - 1	461 ± 67 (295-580)
New Zealand NZ	44° 50' S 176° E	950	January 1994	109	Female - 48 Male - 52	327 ± 62 (174-464)

Table 5.3. Warty oreo. Sample details. N = the number of individuals collected and may include both juvenile fish or fish that were not sexed. Size (standard length) is presented as mean ± standard deviation and range in brackets. na = not available.

Sample and Abbreviation	Location	Depth (m)	Date	No.	Sex	Size (mm)
Western Australia 1 WA 1	23° 58' S 111° 54' E	1065 to 1320	January 1991	47	Female - 21 Male - 7	160 ± 15 (95-184)
Western Australia 2 WA 2	27° 20' S 112° 10' E	945 to 1280	January 1991	34	Female - 18 Male - 6	177 ± 21 (121-217)
Western Australia 3 WA 3	32° 28' S 114° 26' E	614 to 960	February 1991	36	Female - 9 Male - 7	208 ± 34 (121-257)
Western Australia 4 WA 4	35° 06' S 115° 31' E	750	August 1993	154	Female - 93 Male - 43	221 ± 26 (160-298)
Western Australia 5 WA 5	35° 26' S 117° 22' E	900	March 1992	65	Female - 17 Male - 12	178 ± 35 (96-283)
Great Australian Bight GAB	33° 42' S 130° 21' E	850 to 1130	March/ June 1992	137	Female - 97 Male - 55	195 ± 39 (110-286)
Southern Tasmania STAS	44° 09' S 147° 11' E	1020 to 1095	April 1993	111	Female - 61 Male - 38	218 ± 41 (124-302)
New South Wales NSW	33° 58' S 151° 48' E	na	April 1994	32	Female - 15 Male - 10	243 ± 22 (194-290)
Lord Howe Rise LHR	35° 26' S 164° 43' E	935 to 990	June 1992	83	Female - 38 Male - 6	190 ± 44 (109-285)
South Africa S Af	35° 03" S 24° 06' E	na	September 1993	11	Female - 4 Male - 1	229 ± 43 (165-285)

Table 5.4. Spikey oreo. Sample details. N = the number of individuals collected and may include both juvenile fish and individuals that were not sexed. na - data not available. Size (standard length, except NZ total length) is presented as mean ± standard deviation and range in brackets.

Sample and Abbreviation	Location	Depth (m)	Date	N	Sex	Size (mm)
Western Australia 1 WA 1	34° 59' S 114° 42' E	750	February 1991	4	Female - 2 Male - 1	167 ±17 (142-181)
Western Australia 2 WA 2	35° 11' S 118° 49' E	600 to 900	March 1992	3	na	na
Western Australia 3 WA 3	35° 26' S 117° 22' E	900	March 1992	9	Female - 4	252 ± 72 (158-351)
Western Australia 4 WA 4	35° 03' S 114° 55' E	800	May 1992	6	Female - 1 Male - 1	150 ± 15 (137-157)
Western Australia 5 WA 5	35° 06' S 115° 31' E	750	August 1993	8	Female - 3 Male - 2	261 ± 35 (228-325
Western Australia 6 WA 6	34° 45' S 114° 16' E	850	October 1993	118	Female - 58 Male - 6	252± 30 (190-358)
Great Australian Bight 1 GAB 1	33° 57' S 131° 26' E	1000	February 1992	10	Female - 3 Male - 1	202 ± 70 (128-345)
Great Australian Bight 2 GAB 2	33° 47' S 130° 57' E	850 to 930	March 1992	8	Female - 1	160 ± 78 (90-342)
Great Australian Bight 3 GAB 3	33° 45' S 130° 58' E	850	March 1992	9	Female - 3	193 ± 88 (110-360)
Great Australian Bight 4 GAB 4	33° 49' S 131° 14' E	980	June 1992	1	na	165
Great Australian Bight 5 GAB 5	33° 36' S 129° 52' E	960	June 1992	5	Female - 3	175 ± 21 (154-206)
South Australia SA	36° 54' S 137° 20' E	700	October 1993	114	Female - 54 Male - 58	295 ±21 (242-347)
Western Tasmania WTAS	41° 35' S 144° 20' E	540 to 630	May 1993	91	Female - 42 Male - 38	260 ± 27 (183-306)
Southern Tasmania 1 STAS 1	44° 11' S 146° 09' E	750 to 900	March 1994	9	Female - 6 Male - 2	305 ±32 (230-340)
Southern Tasmania 2 STAS 2	44° 15'S 147° 14'E	880	April 1994	36	Female - 16 Male - 20	308 ± 25 (260-370)

Table 5.4. continued.

Sample and Abbreviation	Location	Depth (m)	Date	N	Sex	Size (mm)
Eastern Tasmania 1 ETAS 1	42° 40' S 148° 25' E	440 to 550	July 1993	159	Female - 109 Male - 18	264 ± 28 (192-330)
Eastern Tasmania 2 ETAS 2	42° 42' S 148° 26' E	500	April 1994	115	Female - 74 Male - 40	281 ± 21 (240-370)
Eastern Tasmania 3 ETAS 3	41° 14' S 148° 45' E	585 to 1185	April 1994	35	Female - 23 Male - 11	312 ± 30 (255-400)
Bass Strait BS	39° 03' S 148° 43' E	860	April 1994	6	Female - 4 Male - 2	313 ± 24 (280-355)
New South Wales 1 NSW 1	37° 41' S 150° 20' E	850 to 950	February 1994	50	Female - 21 Male - 28	328 ± 24 (270-380)
New South Wales 2 NSW 2	33° 58' S 151° 48' E	1005	April 1994	9	Female - 1 Male - 5	282 ± 44 (230-335)
Lord Howe Rise LHR	36° S 165° 30' E	740 to 800	August 1993	98	Female - 83 Male - 15	329 ± 25 (260-383)
New Zealand NZ	44° 50' S 176° E	950	January 1994	101	Female - 44 Male - 34	224 ± 65 (101-388)

Table 5.5. Non-commercial oreosomatid species and other species examined for taxonomic and phyogenetic analyses: Sample details. N = number of individuals collected and may include both juvenile fish or fish that were not sexed. na = not available.

Species and Abbreviation	Location	Depth (m)	Date	No.	Sex	Size (mm)
Oreosomatids						
Neocyttus sp. A NA	Southern Tasmania (42° '53 S 147° '20 E)	900 to 1300	May 1993	19	Female - 12 Male - 5	178 ± 18 (141-216)
Neocyttus helgae NH	North Atlantic (61° 39 N 13° 11' W)	1400	February 1993	36	Female - 19 Male - 13	280 ± 43 (153-343)
Oreosoma atlanticum OA	Great Australian Bight	na	March 1992	83	Female - 66 Male - 8	146 ± 14 (112-175)
	Southern Tasmania (44° 12' S 146° 11' E)	na	October 1994	16	na	143 ± 16 (110-175)
	(42° 58' S 144° 59' E)	na	October 1994	3	na	168 ± 25 (140-185)
Non-oreosomatids						
Beryx splendens BS	Western Australia	na	June 1992	6	na	na
Cyttus australis CA	Gabo Island Bass Strait	na	September 1994	6	na	na
Naso tuberosus NT	Queensland	na	March 1994	2	na	na

Table 5.6. Spikey oreo. Points defined for measurement.

Number	Position
1	Snout tip, between anterior tips of lachrymals
2	Beginning of urostyle
3	Anal-fin insertion
4	Dorsal-fin insertion
5	Posterior tip of operculum
6	Dorsal-fin origin
7	Anal-fin origin
8	Anterior margin of eye socket
9	Posterior margin of eye socket
10 & 11	Points at narrowest part of suborbit
12	Posterior tip of maxilla
13	Apex of mandible
14	Posterior tip of lower jaw
15	Pelvic-fin origin
16	Pectoral-fin insertion
17	Second dorsal-fin spine base
18	Second dorsal-fin spine tip
19	First anal-fin spine base
20	First anal-fin spine tip
21	Intersection of line 1-25 by a perpendicular line through point 5
22	Intersection of line 1-25 by a perpendicular line through point 8
23	Intersection of line 16-26 by a perpendicular line through point 7
24	Intersection of a line through point 2, perpendicular to line 1-3, with the ventral margin of the caudal peduncle
25	Placed to create a line through point 1 perpendicular to a line through points 1 and 3
26	Placed to create a line through point 16 parallel to a line through points 1 and 3

Table 5.7. Spikey oreo. Measurements taken for the morphometric analysis.

Measurement	Abbreviation	Points
Standard length	SL	1-2
Head length	HL	21-5
Body depth	BD	6-7
Dorsal base length	DBL	6-4
Anal base length	ABL	7-3
Orbit diameter	OD	8-9
Lachrymal width	LW	10-11
Snout length (horizontal)	SnLH	8-22
Upper jaw length	UJ	1-12
Lower jaw length	LJ	13-14
Pectoral-pelvic distance	PV	15-16
Pectoral-anal distance	PA	7-23
Second dorsal-fin spine height	2DSH	17-18
First anal-fin spine height	1ASH	19-20
Caudal peduncle depth	CPD	3-4
Caudal peduncle length	CPL	3-24
Interorbital width	IOW	Vernier calipers

Table 5.8. Details of enzymes used. Tissue: l - liver, m - muscle. Gel: A - cellulose acetate with a Tris-glycine buffer, B - cellulose acetate with a Tris-citrate buffer, C - starch (see text). Multiple loci encoding for the same enzyme are designated by consecutive numbers, with '1' denoting the fastest migrating system. Locus numbers refer to tables in section 6.3. # = locus not included in phylogenetic analyses.

Enzyme	EC Number	Locus Abbrev.	Locus No.	Tissue	Gel
Aspartate aminotransferase	2.6.1.1	*sAAT-1**	1	m	A
		*sAAT-2**	2	l	A
		*mAAT**	3	m/l	A
Alcohol dehydrogenase	1.1.1.1	*ADH**	4	l	A
Adenylate kinase	2.7.4.3	*AK**	5	m	B
Creatine kinase	2.7.3.2	*CK-A**	6	m	A
Esterase-D (UV, umb. acetate)	3.1.-.-	*ESTD**	7	m/l	A
Fumarate hydratase	4.2.1.2	*FH**	8	m	A
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-1**	9	m	B
		*GAPDH-2**	10	m	B
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A**	#	m	A
		*GPI-B**	11	m	A
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-2**	12	m	B/C
Isocitrate dehydrogenase	1.1.1.42	*sIDHP**	13	m	C
		*mIDHP**	14	l	B
l-Lactate dehydrogenase	1.1.1.27	*LDH-C**	15	l	A
		*LDH-1**	16	l	A
		*LDH-2**	17	m	A
Malate dehydrogenase	1.1.1.37	*sMDH-1**	18	m	C
		*sMDH-2**	19	m	C
Malic enzyme	1.1.1.40	*sMEP**	#	m/l	A
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	20	l	A
Peptidase (l-leucyl-l-tyrosine)	3.4.-.-	*PEP1-1**	21	l	A
Peptidase (leu-leu-leu)	3.4.-.-	*PEP2**	22	l	A
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	23	m	B/C
Phosphoglucomutase	5.4.2.2	*PGM-1**	24	l	A
		*PGM-2**	25	m/l	A
Superoxide dismutase	1.15.1.1	*sSOD**	26	l	A
General Protein		PROT	#	m	A

Table 5.9. The 17 restriction enzymes tested in each species, indicating the 10 that were used in the mitochondrial DNA analyses of each species.

			Enzymes used in each species			
Enzyme	**Site**	**Recognition Site**	**black**	**smooth**	**warty**	**spikey**
Afl II	6	C'TTAAG	-	-	1	1
Apa I	6	GGGCC'C	-	1	-	2
Apa LI	6	G'TGCAC	-	-	2	-
Ava I	5.5	C'PyCGPuG	1	2	3	3
Ban I	5.5	G'GPyPuCC	-	-	4	-
Bgl I	6	GCCNNNN'NGGC	-	-	5	-
Bst EII	6	G'GTNACC	2	3	-	4
Dra I	6	TTT'AAA	3	4	-	-
Eco RI	6	G'AATTC	4	5	6	5
Eco RV	6	GAT'ATC	-	-	7	-
Hind III	6	A'AGCTT	5	6	8	6
Kpn I	6	GGTAC'C	6	-	-	-
Pst I	6	CTGCA'G	7	7	-	7
Pvu II	6	CAG'CTG	8	8	9	8
Sma I	6	CCC'GGG	-	-	-	9
Sty I	5.5	C'CA/TA/TGG	9	9	-	-
Xba I	6	T'CTAGA	10	10	10	10

6. TAXONOMY, SYSTEMATICS AND DISTRIBUTIONS

6.1 DIAGNOSES AND DISTRIBUTION OF AUSTRALASIAN OREOS

Eleven oreosomatids were considered valid worldwide. Although James *et al.* (1988) suggested that *Neocyttus helgae* and/or *N. acanthorhynchus* may be found to be synonymous with *N. rhomboidalis*, the present study suggests that each is valid.

Six species of oreos have now been identified from the Australasian region: *Allocyttus niger* (black oreo), *A. verrucosus* (warty oreo), *Neocyttus rhomboidalis* (spikey oreo), *Oreosoma atlanticum* (oxeye oreo) and *Pseudocyttus maculatus* (smooth oreo); the rough oreo (*N.* sp. A), discovered in the course of this project, is new to science.

The juvenile form of the black oreo, which differs dramatically in shape from the adult, was once considered to be a distinct species. Our findings corroborate those of James *et al.* (1988), who first considered the forms to be conspecific.

A description of the Oreosomatidae and each Australasian species follows. Members of the group change dramatically with age, so juveniles (large and small) are described where specimens and/or published data were available. Descriptions are based on Australian specimens and meristics are only included in diagnoses of adult specimens.

Oreosomatidae
(Oreos)

Type species.—*Oreosoma atlanticum* Cuvier, 1829

Diagnosis.—ADULTS: body short, very deep, mostly rhomboidal (sometimes oval), laterally compressed; head rather large, thicker than body; eye relatively large to huge; mouth upturned, strongly protractile; scales cycloid or ctenoid, often finely spinulated; adherent scales on predorsal area (nape); dorsal and anal fin with strong spines in most species, some lockable in erect position; dorsal fin with 5–9 spines, 27–36 soft rays; anal fin with 2–4 spines, 25–34 rays; pelvic fin with one strong spine, 5–7 soft rays; pectoral fin with 16–22 rays; caudal fin with 11 branched rays flanked either side by a simple ray and 2–3 procurrent rays; gill rakers 20–34; vertebrae 34–43. Colour drab, varying from bluish to brownish shades of grey or black.

JUVENILES AND SUB-ADULTS: differing greatly in body shape from adult, often with a late metamorphosis (up to about 200 mm TL); abdomen usually greatly expanded, almost bulbous; small to huge conical scutes mostly present on body; colour similar to adults but some with pattern of blotches.

Size.—Maximum sizes for oreo species range from 177 mm SL (about 210 mm TL) in *Oreosoma* to 583 mm SL (about 680 mm TL) in *Pseudocyttus*.

Distribution.—Marine in tropical to high latitudes. Known from the Pacific, Indian, Atlantic and Southern Oceans. Most prevalent in temperate seas of the Southern Hemisphere.

Remarks.—Oreo dories belong to a group of fishes collectively known as the Order Zeiformes, or dories. The evolutionary relationships of the family are not fully understood with several schools of thought on the matter. Possibly the most plausible scheme was proposed by Johnson and Patterson (1993) in which 5 families are recognised within a monophyletic suborder, the zeioids (i.e. families Parazenidae, Macrurocyttidae, Zeidae, Grammicolepidae, and Oreosomatidae). The family Caproidae, which has been traditionally considered to be related, is given separate provisional subordinal placement in the order. All of these families are represented in the Australasian region and some are of commercial value.

Members of the family Oreosomatidae are distinct from the members of related families. However, current generic placements are probably inappropriate and are in need of revision (James *et al.*, 1988; Lowry *et al.*, 1996). All four genera (*Neocyttus*, *Allocyttus*, *Pseudocyttus*, and *Oreosoma*) and six of the 11 known species occur in Australasian waters.

Allocyttus niger James, Inada & Nakamura, 1988 (Black Oreo)

Figure 6.1

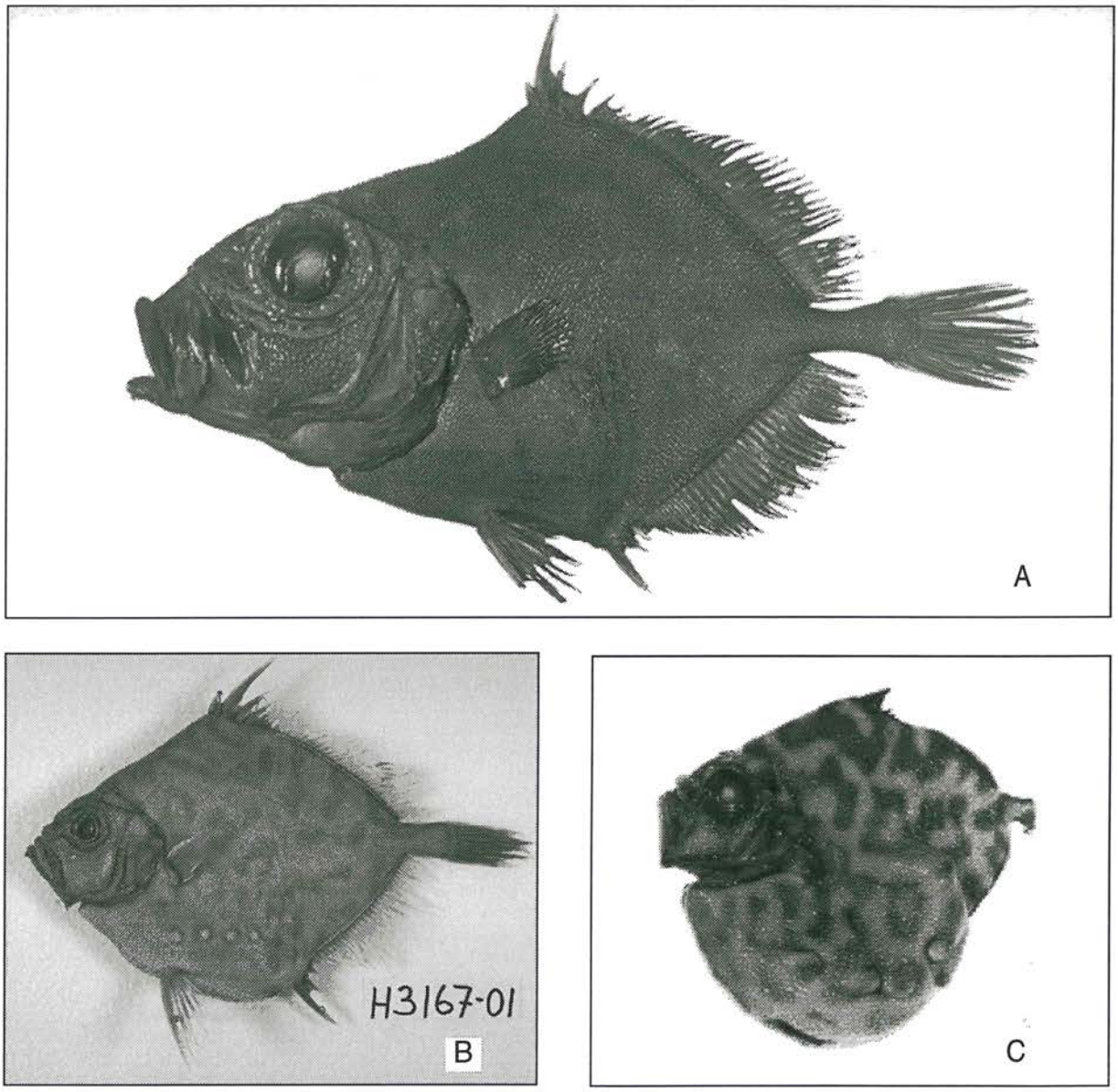


Figure 6.1. Black oreos, *Allocyttus niger*: A—adult, CSIRO H3972.02, 282 mm SL; B—large juvenile, CSIRO H3167.01, 193 mm SL; C—small juvenile, NMNZ P15947, 37 mm SL.

Holotype.—*Allocyttus niger* James, Inada and Nakamura, 1988, NMNZ P15939, 295 mm SL, Chatham Rise, New Zealand, 44°06'S, 178°24'E, 960–1015 m, 14 Dec. 1981.

Description.—ADULTS (specimens examined 222–282 mm SL): body rhomboidal, depth 61.1–65.2% SL; predorsal profile moderately concave behind eye, predorsal length 52.9–59.0% SL; head large, length 35.6–39.1% SL, width 20.9–23.3% SL; eye diameter large, 16.5–21.1% SL; dorsal-fin with 37–41 spines and rays, second spine greatly enlarged, about half as high again as third spine, height 14.4–17.7% SL, maximum length 2.1–2.8%SL, about 3.4 times first spine; anal-fin spines and rays 32–34, first spine

greatly enlarged, about half as high again as second spine; 6 pelvic fin rays, pelvic-fin spine very high, extending well beyond anal opening, usually beyond anal-fin origin; distance from pelvic-fin insertion to anal-fin origin 15.5–19.8% SL; 18–21 pectoral fin rays; scales very adherent, those between pectoral fin and lateral line upright, ctenoid, with 1–3 ctenii, the central longest; opercles with triangular patch of 11–14 spinulate ridges; snout mostly scaled, scales more sparse in larger specimens, naked area immediately anterior to eye; head bones with ridges and spinules; abdomen with protuberance scars, sometimes absent in larger specimens; body dark greyish brown, dark grey or black; fins and mouthparts black; 39–41 vertebrae.

LARGE JUVENILES (specimens examined 192–217 mm SL): body rhomboidal, depth 70.5–73.0% SL; predorsal profile almost straight behind eye, predorsal length 50.5–54.3% SL; head large, length 31.7–32.7% SL, width 19.7–22.1% SL; eye diameter small, 12.1–15.2% SL; dorsal-fin second spine greatly enlarged, about half as high again as third spine, height 17.7–19.5% of SL, maximum length 2.5–3.0%SL, about 3.0 times first; first anal-fin spine greatly enlarged, about half as high again as second spine; pelvic-fin spine very high, extending to or beyond anal opening; distance from pelvic insertion to anal-fin origin 24.2–29.1% SL; scales extremely adherent, those between pectoral fin and lateral line ctenoid with 3–5 ctenii, central largest; opercles with triangular patch of 11–14 spinulate ridges; snout mostly scaled (with small naked area immediately anterior to eye); head bones mostly with ridges and spinules; abdomen with row of four scaled protuberances and a fifth protuberance dorsal to the posterior end of the row; body pale bluish or greyish with darker irregular blotches and reticulations.

SMALL JUVENILES (specimens <147 mm SL, data from James *et al.* (1988)): body subcircular, depth 80.6–94.6% SL; predorsal profile almost straight behind eye, predorsal length 52.5–57.0% SL; head large, length 32.8–39.2% SL; eye diameter small, 11.2–13.8% SL; dorsal-fin second spine enlarged, height 9.7–18.3% of SL, about 2.4 times first; first anal-fin spine enlarged; pelvic-fin spine high, extending to anal opening in larger specimens; scales extremely adherent, those between pectoral fin and lateral line cycloid; opercles with triangular patch of ridges; abdomen with row of four scaled protuberances and a fifth protuberance dorsal to the posterior end of the row; body pale bluish or greyish with darker irregular blotches and reticulations.

Size.—Reaches a SL of 395 mm (490 mm TL).

Distribution.—Adults are found off eastern and southern New Zealand and southern Australia (Woollongong, New South Wales to Cape Naturaliste, Western Australia, including Tasmania) and associated seamounts (e.g. Cascade Plateau, Challenger Plateau, Chatham Rise, Macquarie Ridge, Puysegur Bank, South Tasman Rise) in depths between 510–1300 m (Figure 6.2). The continuity of their distribution is unknown.

Records off Tasmania's west coast are of large juveniles; no adults have been recorded from that region. Large juveniles are also recorded from off southern Tasmania and the South Tasman Rise, but small juveniles are only known from New Zealand. There are no records of *A. niger* outside Australasian waters.

Remarks.—*Allocyttus* contains four described species (Table 2.1). James *et al.* (1988) placed *A. niger* in this genus but stated that oreosomatid genera require redefinition. They did not have specimens of *A. folletti* Myers, 1960 or *A. guineensis* Trunov and Kukuev *in* Trunov, 1982 to compare with their new species.

A. niger is distinct from its three congeners. Adult specimens have: a more rhomboidal body; higher, more robust fin spines (e.g. the height of the undamaged second dorsal-fin spine is 14.4–17.7% SL in *A. niger* and 3.9–12.6% SL in its congeners); scaled

Figure 6.2. Australasian distribution (black shading) of black oreo, *Allocyttus niger*. The dotted lines show the 1500 m contour, question marks indicate regions of suspected, though not confirmed, distribution and arrows highlight small distribution patches.

abdominal protuberances (compared with one enlarged, modified scale forming the majority of each protuberance or wart in other *Allocyttus* species); more gill rakers on the first arch (28–31 in *A. niger* compared with 20–26 in its congeners); and more vertebrae (39–41 in *A. niger* compared with 36–39 in its congeners).

A. niger differs from its only Australasian congener, *A. verrucosus*, in having: a more rhomboidal body; higher fin spines (e.g. second dorsal-fin spine 14.4–17.7% SL compared with 5.4–9.1% SL in *A. verrucosus*); a shorter pelvic-anal interspace (distance from pelvic-fin insertion to anal-fin origin 15.5–19.8% SL compared with 19.2–23.1% SL in *A. verrucosus*); and more dorsal-fin elements (37–41 compared with 35–37 in *A. verrucosus*).

Genetic evidence (Lowry *et al.*, 1996, see section 6.3) suggests that this species may be more akin to *Neocyttus* than to *A. verrucosus*, a proposal supported by morphological and meristic data here. However, adults differ from *N. rhomboidalis* adults, with which they have been confused, in having: a moderately concave predorsal profile behind the eye (very concave in *N. rhomboidalis*); fewer anal-fin elements (32–34 compared with 33–38 in *N. rhomboidalis*); and more gill rakers on the first arch (28–31 compared with 21–25 in *N. rhomboidalis*). Juveniles differ in having prominent abdominal protuberances (absent in *N. rhomboidalis*).

A. niger juveniles differ markedly from the adults (e.g. more rhomboidal or subcircular body, smaller eye, higher fin spines) and, compared with other oreos, metamorphose at a large size (about 220–225 mm SL). The juveniles are probably pelagic.

Allocyttus verrucosus (Gilchrist, 1906)
(Warty Oreo)
Figure 6.3

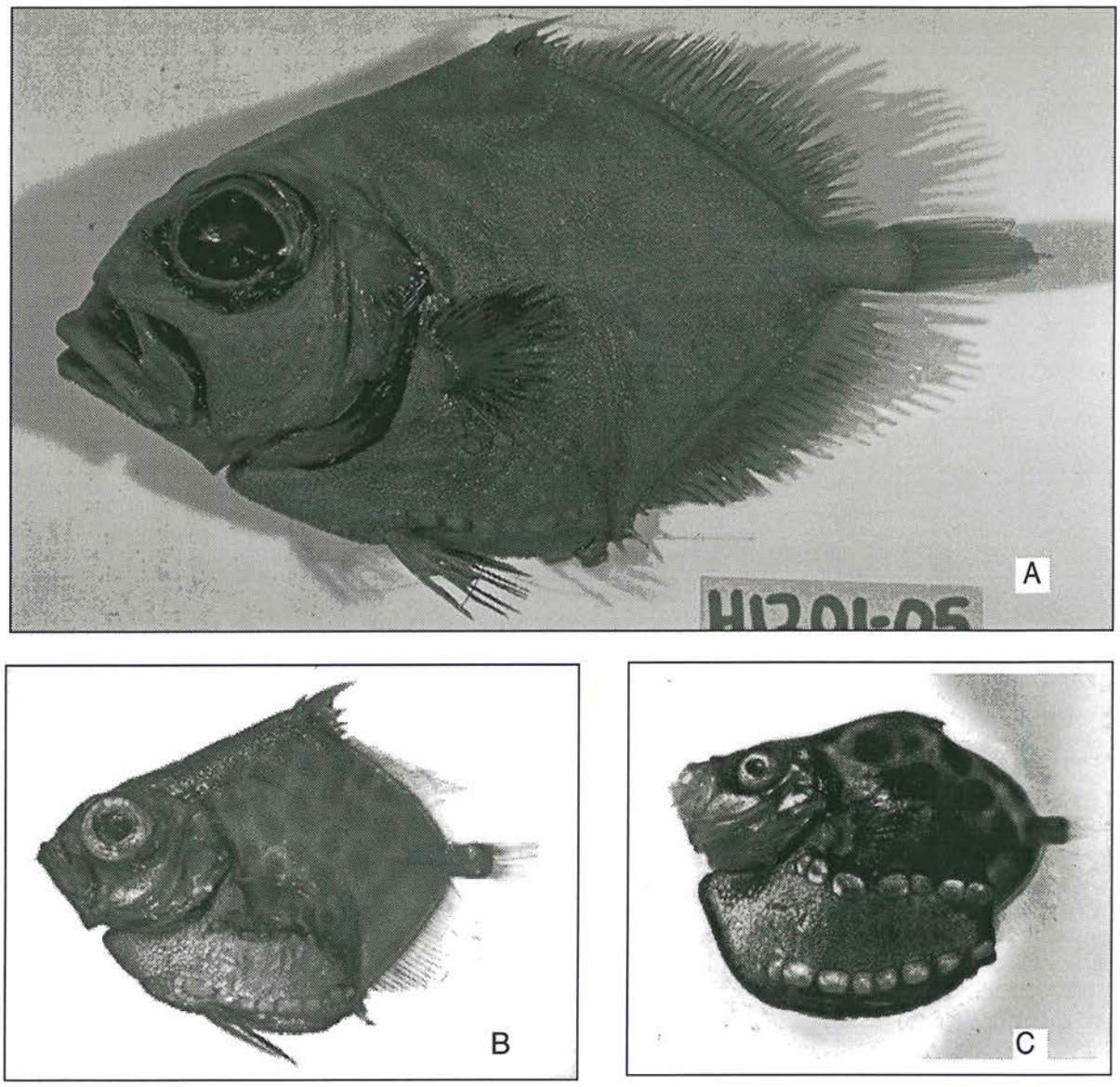


Figure 6.3. Warty oreos, *Allocyttus verrucosus*: A—adult, CSIRO H1201.05, 185 mm SL; B—large juvenile, CSIRO H1544.01, 92 mm SL; C—small juvenile, NMNZ P15959, 35.5 mm SL.

Holotype.—*Cyttosoma verrucosum* Gilchrist, 1906, SAM, specimen probably lost, off Cape Point, South Africa, about 34°20'S, 18°20'E, 1100 m, date unknown.

Allocyttus verrucosus var *propinquus* McCulloch, 1914, specimen lost, Great Australian Bight, about 34°30'S, 129°28'E, 640–825 m, 14 May 1913.

Description.—ADULTS (specimens examined 204–274 mm SL): body slightly rhomboidal to oval, depth 53.1–68.0% SL; predorsal profile very slightly concave behind eye, predorsal length 51.0–58.4% SL; head very large, length 36.6–41.9% SL, width 20.8–27.4% SL; eye diameter large, 17.6–20.6% SL;

dorsal-fin with 35–37 spines and rays, second spine very slightly enlarged, slightly higher than third spine, height 5.4–9.1% SL, maximum length 0.8–1.6%SL, about 5.0 times first spine; anal-fin spines and rays 29–31, first spine slightly enlarged, slightly higher than to about half as high again as second spine; 6 (rarely 5) pelvic fin rays, pelvic-fin spine high, extending about half to three quarters distance from pelvic-fin spine origin to anal opening; distance from pelvic-fin insertion to anal-fin origin 19.2–23.1% SL; 17–19 pectoral fin rays; scales adherent, those between pectoral fin and lateral line ctenoid, with 5–9 ctenii, the central sometimes slightly longer than others; opercles with triangular patch of 12–17 spinulate ridges; snout naked; head bones with ridges and spinules; abdomen with 2 rows of warts (enlarged modified scales), variable in number and development; body darkish brown, sometimes greyish; fins and mouthparts darker, sometimes almost black; 36–38 vertebrae.

LARGE JUVENILES (specimens examined 81–93 mm SL): body moderately rhomboidal to subcircular, depth 66.9–78.2% SL; predorsal profile very slightly concave behind eye, predorsal length 60.2–63.2% SL; head large, length 39.4–42.7% SL, width 21.4–24.3% SL; eye diameter large, 19.3–21.9% SL; second dorsal-fin spine greatly enlarged, half or more as high again as third spine, height 11.8–15.9% SL, maximum length 2.1–2.8% SL, about 2.8 times first spine; first anal-fin spine enlarged, almost twice as high as second spine; pelvic-fin spine high, extending almost to anal opening; distance from pelvic-fin insertion to anal-fin origin 26.7–35.0% SL; scales very adherent, those between pectoral fin and lateral line cycloid; opercles with triangular patch of about 16–18 sparsely spinulate ridges; snout naked; head bones with ridges and a few spinules; abdomen with 2 rows of warts (enlarged modified scales), variable in number and development; body pale to dark greyish brown with bluish black blotches; fins and mouthparts greyish brown to dark grey.

SMALL JUVENILES (<35 mm SL, data from James *et al.* (1988)): body subcircular, depth 84.5% SL; predorsal profile very slightly concave behind eye, predorsal length 62.0% SL; head large, length 41.4% SL; eye diameter large, 15.5% SL; second dorsal-fin spine enlarged, height 7.9% SL, about 1.8 times first spine; pelvic-fin spine low; scales adherent, those between pectoral fin and lateral line cycloid; opercles with triangular patch of radiating ridges; abdomen with 2 rows of warts (enlarged modified scales); body silvery with dark blotches on upper half; fins mostly translucent.

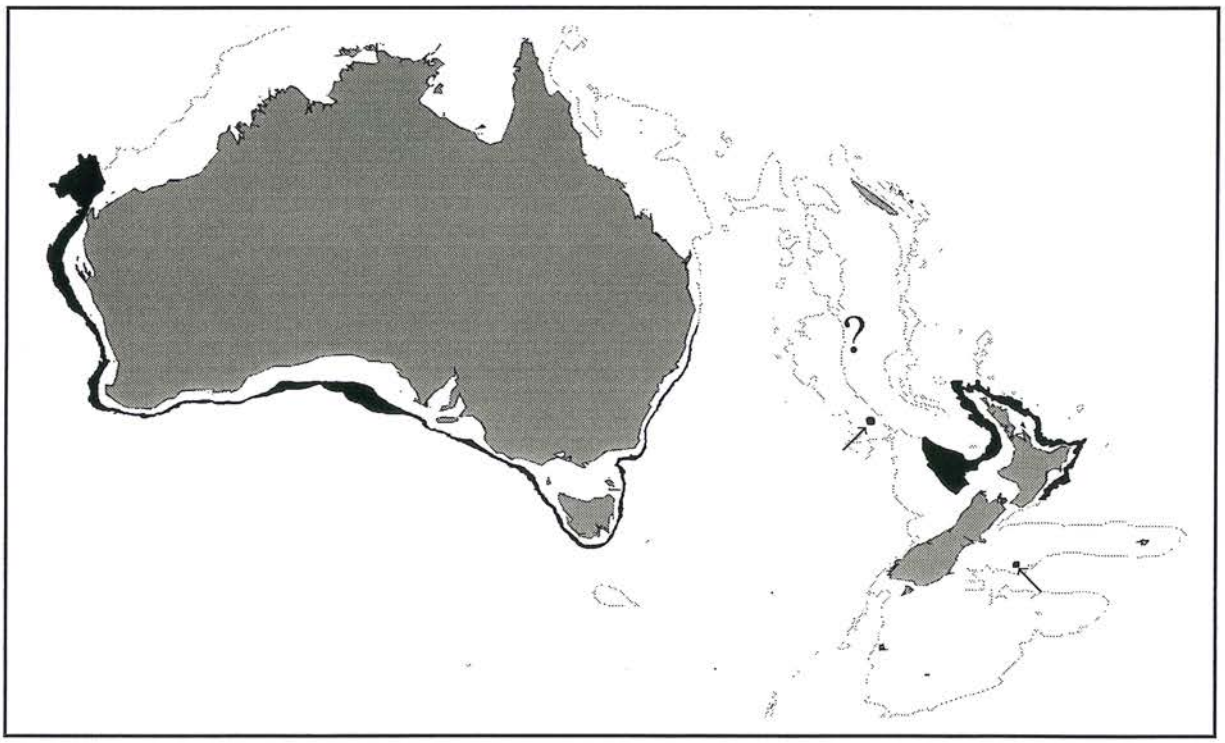


Figure 6.4. Australasian distribution (black shading) of warty oreo, *Allocyttus verrucosus*. The dotted lines show the 1500 m contour, question marks indicate regions of suspected, though not confirmed, distribution and arrows highlight small distribution patches.

Size.—Reaches 305 mm SL (370 mm TL).

Distribution.— In Australasia, recorded from off southern Australia (from Coffs Harbour, New South Wales, to Onslow (about 18°S), Western Australia, including Tasmania) and off New Zealand (including Challenger Plateau, Chatham Rise, Lord Howe Rise and Louisville Ridge) (Figure 6.4). Elsewhere this species has been taken from the western and eastern South Atlantic, the southern North Atlantic and off southern Africa.

Remarks.—*A. verrucosus* is morphologically and meristically similar to *A. guineensis* and, in particular, *A. folletti*. It differs from the latter in having: a wider lachrymal (3.3–4.0% SL compared with 1.7–2.4% SL in *A. folletti*); lower fin spines (e.g. second dorsal-fin spine 5.4–9.1% SL compared with 7.6–12.6% SL in *A. folletti*); lower combined dorsal-fin spine and ray count (35–37 compared with 38–39 in *A. folletti*); lower anal-fin spine and ray count (29–31 compared with 31–34 in *A. folletti*); and lower pectoral-fin ray count (17–19 compaed with 19–21 in *A. folletti*). *A. guineensis* is distinguished from both *A. verrucosus* and *A. folletti* in having a lower second dorsal-fin spine (3.9% SL compared with 5.4–12.6% SL in *A. verrucosus* and *A. folletti*) and a larger pelvic-anal distance (25.2% SL compared with 13.9–23.1% SL in *A. verrucosus* and *A. folletti*).

Neocyttus rhomboidalis Gilchrist, 1906
(Spikey Oreo)
Figure 6.5

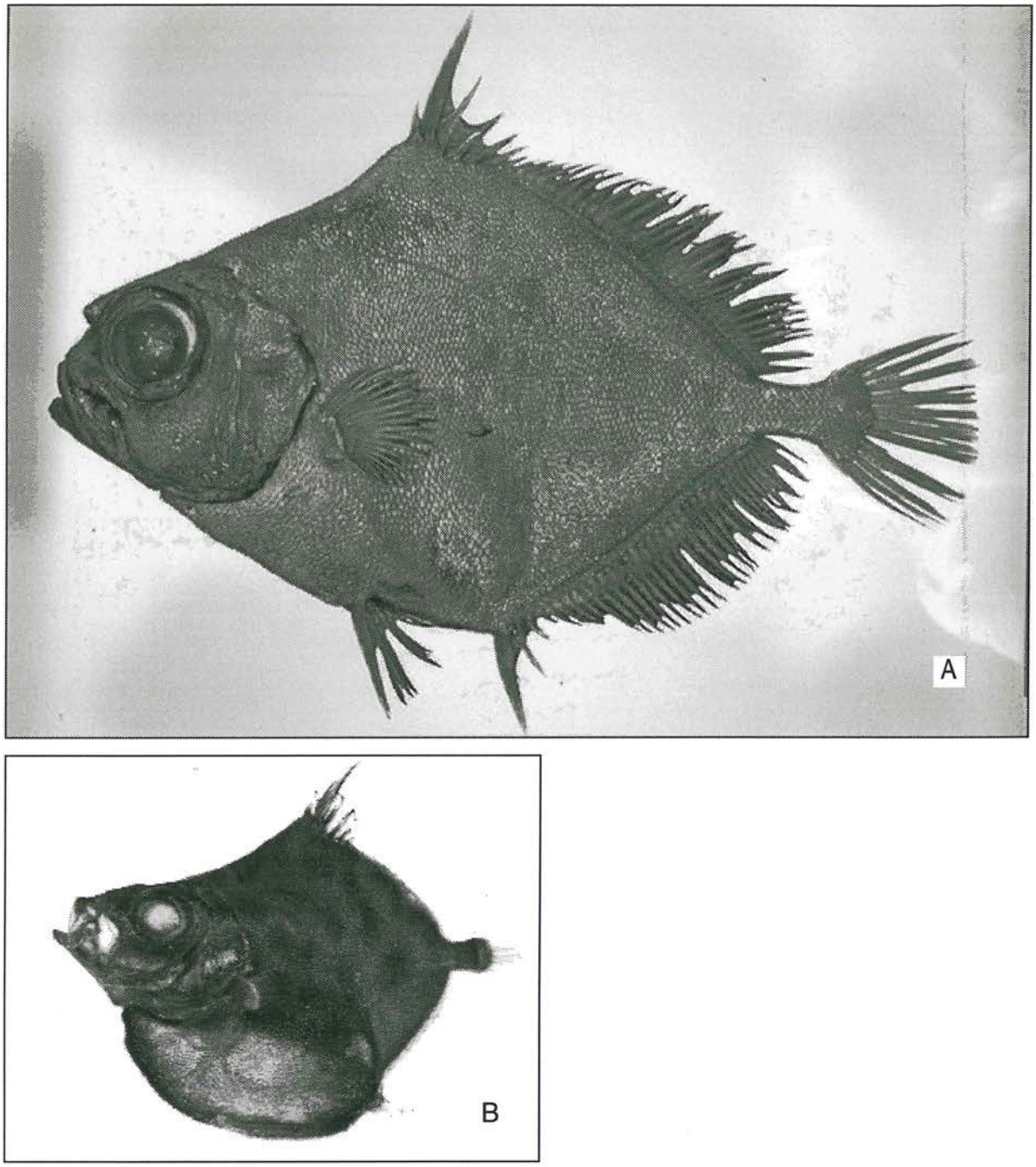


Figure 6.5. Spikey oreos, *Neocyttus rhomboidalis*: A—adult, CSIRO H884.03, 260 mm SL; B—small juvenile, NMNZ P15954, 61.5 mm SL.

Holotype.—*Neocyttus rhomboidalis* Gilchrist, 1906, SAM 11972, 137 mm SL, off Cape Point, South Africa, about 34°18'S, 18°22'E, 575–730 m, 16 Sep. 1903.

Neocyttus rhomboidalis var *gibbosus* McCulloch, 1914, specimen lost, Great Australian Bight, about 34°30'S, 129°28'E, 640–825 m, 14 May 1913.

Description.—ADULTS (specimens examined 178–333 mm SL): body rhomboidal, depth 61.9–75.0% SL; predorsal profile very concave behind eye, predorsal length 49.7–57.9% SL; head moderately large, length 33.8–37.8% SL, width 20.4–23.2% SL; eye diameter large, 16.3–19.0% SL; dorsal-fin with 38–41 spines and rays, second spine greatly enlarged, up to two thirds as high again as third spine, height 14.2–17.2% SL, maximum length 1.9–2.8% SL, about 4.2 times first spine; anal-fin spines and rays 33–38, first spine greatly enlarged, up to two thirds as high again as second spine; 6 pelvic fin rays, pelvic-fin spine very high, extending beyond anal opening, sometimes to origin of second anal-fin spine; distance from pelvic-fin insertion to anal-fin origin 13.5–18.7% SL; 19–21 pectoral fin rays; scales slightly deciduous, those between pectoral fin and lateral line slightly upright, ctenoid, with 12–16 small ctenii; opercles with triangular patch of about 20 bluntly spinulate radiating ridges; snout mostly scaled, sometimes with small naked area immediately anterior to eye and around nostrils; head bones with spinulate ridges; abdomen without protuberances, warts or scars; body light brown to greyish; fins and mouthparts greyish to bluish black; 39–41 vertebrae.

LARGE JUVENILES (specimens examined 85–115 mm SL): body very rhomboidal, depth 72.8–79.8% SL; predorsal profile very concave behind eye, predorsal length 56.0–60.4% SL; head large, length 37.0–41.6% SL, width 21.1–23.5% SL; eye diameter large, 19.9–23.4% SL; second dorsal-fin spine greatly enlarged, about half as high again as third spine, height 18.7–25.8% SL, maximum length 2.9–3.6% SL, about 3.3 times first spine; first anal-fin spine greatly enlarged, nearly twice as high as second spine; pelvic-fin spine high, usually extending beyond anal-fin origin, sometimes to origin of fourth anal-fin spine; distance from pelvic-fin insertion to anal-fin origin 15.8–21.0% SL; scales slightly deciduous, those between pectoral fin and lateral line slightly upright, ctenoid, with 8–11 small ctenii; opercles with triangular patch of 14–18 spinulate radiating ridges (some ridges incomplete, spinules sparse in some specimens); snout mostly scaled, sometimes with small naked area immediately anterior to eye and around nostrils; head bones ridged, with some spinules; abdomen without protuberances, warts or scars; body light brown to greyish; fins and mouthparts greyish to bluish black.

SMALL JUVENILES (<61 mm SL, data from James *et al.* (1988)): body rhomboidal, depth 84.6% SL; predorsal profile very concave behind eye, predorsal length 57.2% SL; head large, length 40.7% SL; eye diameter large, 16.3% SL; second dorsal-fin spine greatly enlarged, height 22.6% SL, about 3.0 times first spine; first anal-fin spine greatly enlarged; pelvic-fin spine high, extending two thirds of distnca from spine origin to anal opening; scales adherent, those between pectoral fin and lateral line cycloid; opercles with triangular patch of radiating ridges; abdomen without protuberances, warts or scars; body bluish grey with darker blotches; fins mostly translucent.

Size.—Reaches 400 mm SL (475 mm TL).

Distribution.—Recorded from off southern Australia (from about Cape Hawke, New South Wales, to Shark Bay, Western Australia, including Tasmania) and New Zealand, and nearby seamounts (Cascade Plateau, Challenger Plateau, Chatham Rise, Lord Howe Rise, Louisville Ridge and South Tasman Rise) in the Australasian region (Figure 6.6). Elsewhere recorded from off southern Africa and Argentina.

Remarks.—*Neocyttus* consists of three described species plus two undescribed species identified as new to science during this study (Table 2.1). Only *N. rhomboidalis* and *N.* sp. A are recorded from Australasian waters. *N. rhomboidalis* has: a narrower lachrymal (2.2–3.6% SL compared with 3.7–5.1% SL in *N.* sp. A); more dorsal-, anal- and pectoral-fin elements (38–41, 33–38 and 19–21 respectively compared with 36–39, 30–34 and 16–18 respectively in *N.* sp. A); less upright body scales; less spinulate head bones; a scaled snout (naked in *N.* sp. A); and more vertebrae (39–41 compared with 37–39 in *N.* sp A).

Figure 6.6. Australasian distribution (black shading) of spikey oreo, *Neocyttus rhomboidalis*. The dotted lines show the 1500 m contour and arrows highlight small distribution patches.

N. rhomboidalis is morphologically and genetically very similar to the North Atlantic *N. helgae* (Holt and Byrne, 1908). James *et al.* (1988) suggested that further study may show these to be synonymous but, although they are closely related (genetic identity of 0.97, on a scale of 0–1), adult *N. rhomboidalis* differ from adult *N. helgae* in having: a shallower body (69.0–83.4% SL in *N. helgae*), a larger eye (12.0–15.7% SL in *N. helgae*), a higer second dorsal-fin spine (12.0–14.5% SL in *N. helgae*) and more pectoral-fin rays (19–21 cf 15–19 in *N. helgae*).

Neocyttus sp. A
(Rough Oreo)
Figure 6.7

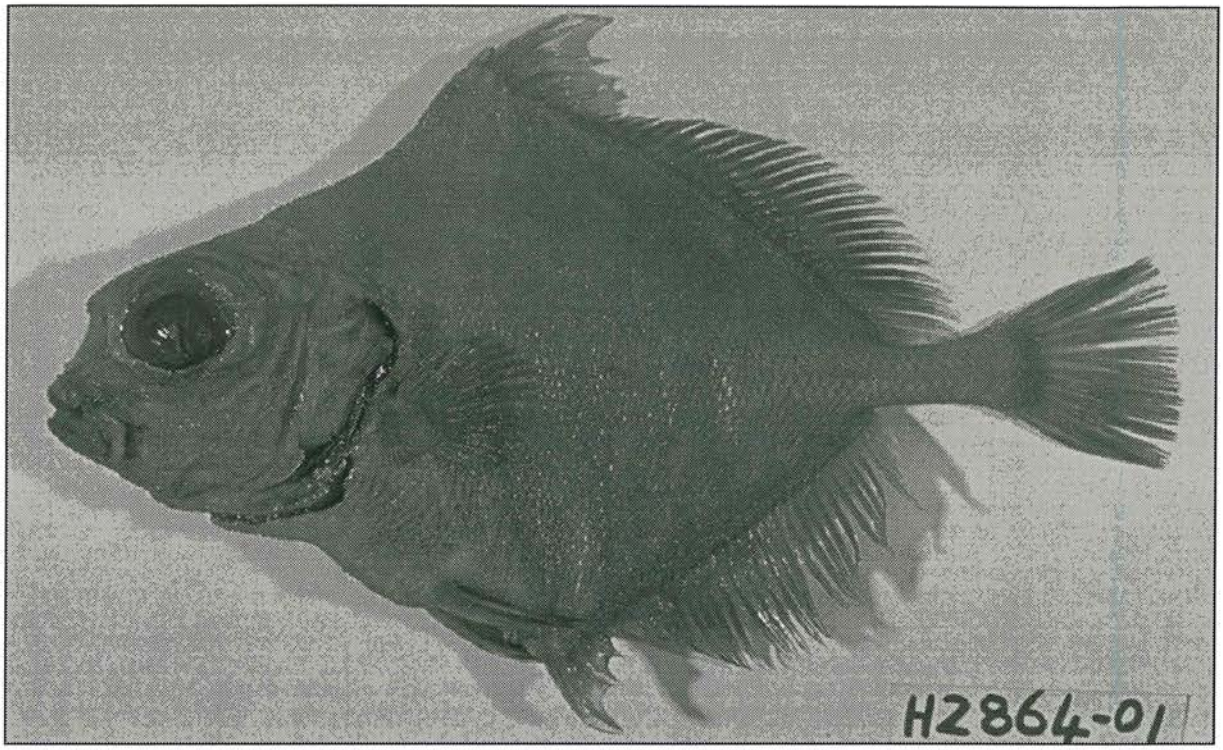


Figure 6.7. Rough oreo, *Neocyttus* sp. A: adult, CSIRO H2864.01, 153 mm SL.

Description.—ADULTS (specimens examined 115–201 mm SL): body moderately rhomboidal, depth 63.3–77.1% SL; predorsal profile very concave behind eye, predorsal length 49.9–56.9% SL; head large, length 31.9–38.4% SL, width 17.7–21.9% SL; eye diameter moderately large, 14.0–18.5% SL; dorsal-fin with 36–39 spines and rays, second spine moderately enlarged, about a third as high again as third spine, height 13.5–17.3% SL, maximum length 1.6–2.5% SL, about 4.3 times first spine; anal-fin spines and rays 30–34, first spine enlarged, about one third to a half as high again as second spine; 5–7 (usually 6) pelvic-fin rays, pelvic-fin spine high, extending to about third anal-fin spine; distance from pelvic-fin insertion to anal-fin origin 11.2–21.6% SL; 16–18 pectoral fin rays; scales very adherent, those between pectoral fin and lateral line upright, ctenoid, with 7–11 ctenii of about equal length; opercles with triangular patch of 14–17 spinulate ridges (each ridge consisting of a row of short, detached nodular spinules); snout naked; head bones extremely spinulate and with some ridges; abdomen without protuberances, warts or scars; body pale to greyish brown; fins and mouthparts bluish black; 37–39 vertebrae.

JUVENILES: No juveniles have been recorded.

Size.—Reaches at least 201 mm SL (about 240 mm TL).

Distribution.—Collected south of Tasmania (Pedra Branca Seamount and South Tasman Rise) and off southwestern Western Australia in depths of 750–1300 m (Figure 6.8). Despite numerous scientific expeditions in deepwater off New Zealand, this species has not been recorded from there.

Remarks.—*Neocyttus* sp. A was identified as new to science during this study. A formal description, including comparisons with its congeners, is in preparation by Yearsley and Last.

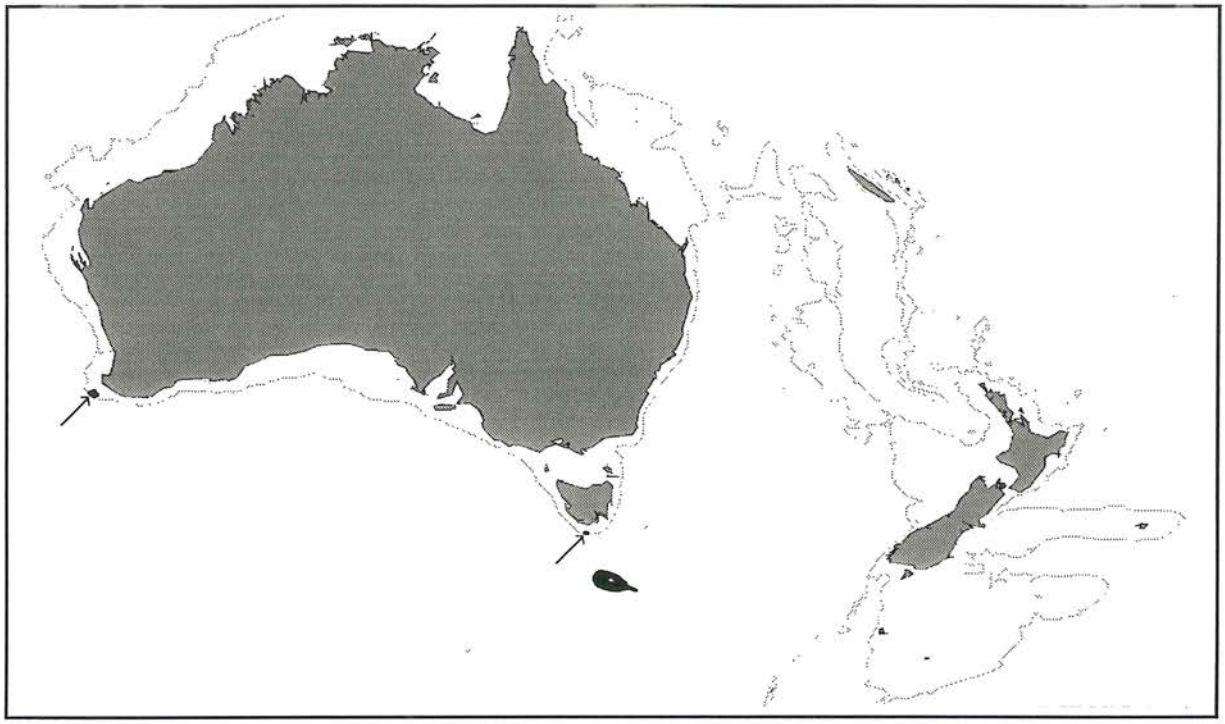


Figure 6.8. Australasian distribution (black shading) of rough oreo, *Neocyttus* sp. A. The dotted lines show the 1500 m contour and arrows highlight small distribution patches.

N. sp. A can be distinguished from its congeners in the following ways.

N. helgae is a larger species than *N.* sp. A and also has: a mostly scaled snout (naked in *N.* sp. A); a larger pectoral–anal distance (28.7–33.0% SL compared with 20.0–28.4% SL in *N.* sp. A); and more vertebrae (39–40 compared with 37–39 in *N.* sp. A).

The Indian Ocean *N. acanthorhynchus* possesses distinctive spines protruding from the lachrymals near the snout and above the eye. Other features which distinguish *N. acanthorhynchus* from *N.* sp. A include: a shallower body (60.8–62.9% SL compared with 63.3–77.1% SL in *N.* sp. A); a shorter snout (direct snout length 6.8–7.7% SL compared with 7.8–9.3% SL in *N.* sp. A); a higher pelvic-fin spine (18.8% SL compared with 13.6–18.3% SL in *N.* sp. A); and a few scales near orbit rim (naked in *N.* sp. A).

See "Remarks" section for *N. rhomboidalis* for a comparison of the two Australasian *Neocyttus* species.

During the preparation of this report, a second undescribed *Neocyttus* species was identified from one specimen off Indonesia in the northeastern Indian Ocean. *N.* sp. B differs from *N.* sp. A in having: a slightly shorter upper jaw (11.4% SL compared with 11.8–14.4% SL in *N.* sp. A); a longer preanal distance (66.4% SL compared with 58.8–64.9% SL in *N.* sp. A); a shorter thoracic ridge (23.6% SL compared with 24.0–28.2% SL in *N.* sp. A); and most of the snout covered by bulbous lachrymal extensions (partly covered in *N.* sp. A). Further specimens are required for a formal description of *N.* sp. B.

Oreosoma atlanticum Cuvier, 1829
(Oxeye Oreo)
Figure 6.9

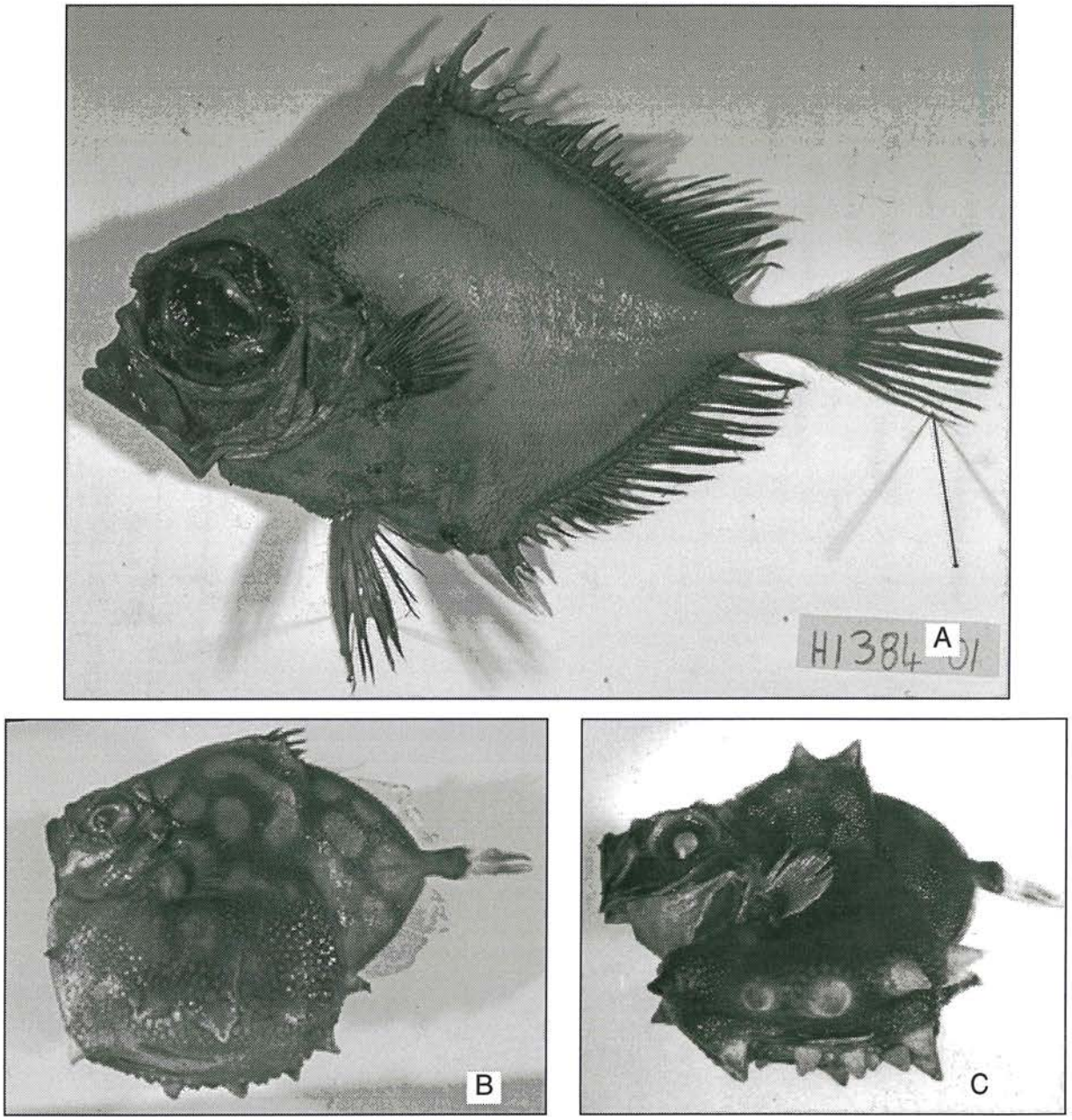


Figure 6.9. Oxeye oreos, *Oreosoma atlanticum*: A—adult, CSIRO H1384.01, 106 mm SL; B—large juvenile, CSIRO H2514.01, 81 mm SL; C—small juvenile, NMNZ P15953, 42.7 mm SL.

Holotype.—*Oreosoma atlanticum* Cuvier *in* Cuvier and Valenciennes, 1829, MNHNP 2242, Atlantic Ocean, possibly 30°S, 10°E.

Cyttosoma boops Gilchrist, 1904, SAM 11971, off Cape Point, South Africa, about 34°15'S, 18°25'E, 220 m.

Oreosoma waitei Whitley, 1929, NMNZ 527, washed up in Lyall Bay, New Zealand.

Description.—ADULTS (specimens examined 99–164 mm SL): body rhomboidal, depth 65.8–77.6% SL; predorsal profile very concave behind eye, predorsal length 45.6–56.0% SL; head large, length 32.6–39.6% SL, width 22.3–25.3% SL; eye diameter huge, 19.6–23.2% SL; dorsal-fin with 35–37 spines and rays, second spine slightly enlarged, about equal in length to third spine, height 12.6–15.8% SL, maximum length 1.2–1.7% SL, height about 2.8 times height of first spine; anal-fin spines and rays 31–32, first spine slightly enlarged, slightly higher than second spine; 5–7 (usually 6) pelvic fin rays, pelvic-fin spine extremely high, extending well beyond anal-fin origin, sometimes to origin of first anal-fin ray; distance from pelvic-fin insertion to anal-fin origin 15.4–22.0% SL; 20–22 pectoral fin rays; scales mostly deciduous, those between pectoral fin and lateral line cycloid or with about 5 minute ctenii; opercles with very prominent enlarged spinulate horizontal ridge; snout mostly naked, with small patch of scales anterior to eye; head bones with ridges and spinules; abdomen smooth, protuberance scars visible in smaller specimens; body dark sandy to purplish brown; fins darker, almost black; mouthparts usually pale brown to grey; 37–39 vertebrae.

JUVENILES (specimens examined 31–81 mm SL): body subcircular, depth 63.1–76.7% SL; predorsal profile almost straight behind eye, predorsal length 51.9–62.9% SL; head large, length 32.7–40.7% SL; eye diameter large, 16.2–21.9% SL; second dorsal-fin spine very slightly enlarged, slightly higher than third spine, height 2–3 times height of first spine; first anal-fin spine enlarged, about one third as high again as second spine; pelvic-fin spine high, extending about four fifths of distance from pelvic-fin origin to anal opening; distance from pelvic-fin insertion to anal-fin origin 40.7–52.5% SL; scales very adherent, those between pectoral fin and lateral line cycloid; opercles with prominent spinulate horizontal ridge; snout naked; head bones with ridges and spinules; abdomen with a row of fivr large conical protuberances and two similar protuberances ventral to row and additional five or more protuberances between pelvic fins; most abdominal scales enlarged; body bluish-black with paler blotches, larger specimens paler with brownish abdomen, protuberances dark grey to brown; fins pale.

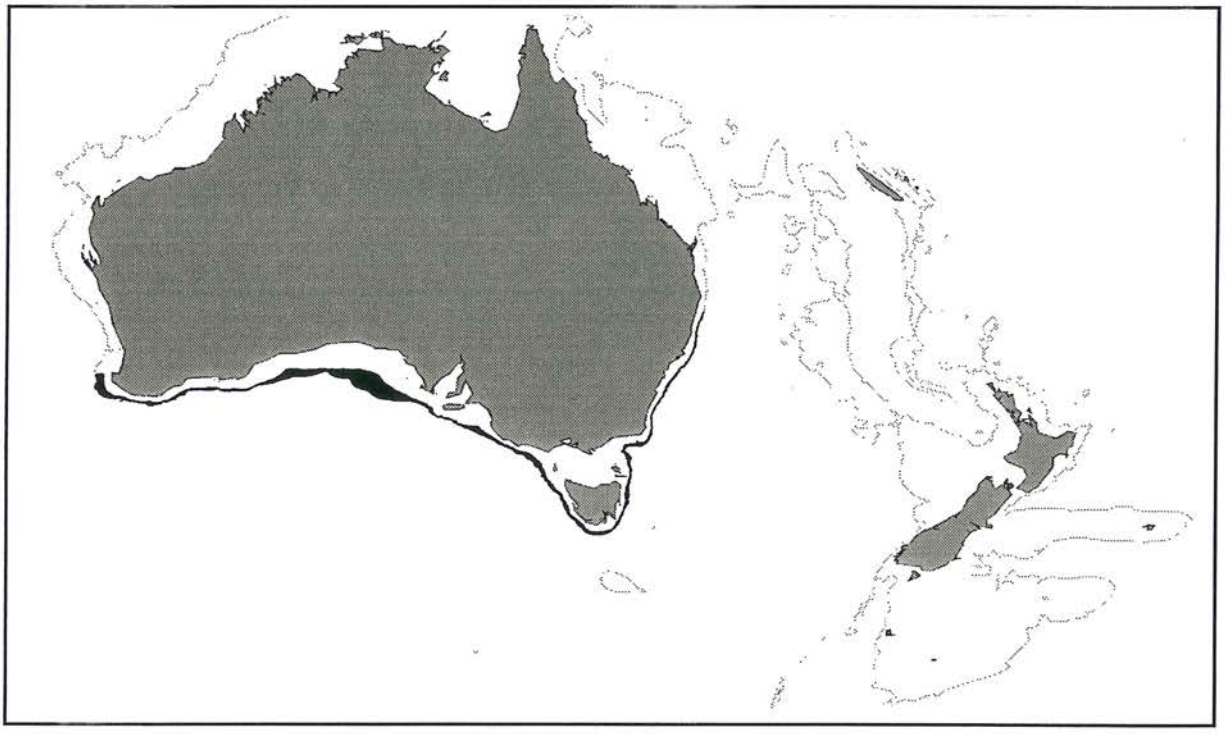


Figure 6.10. Australasian distribution (black shading) of adult oxeye oreo, *Oreosoma atlanticum*. The dotted lines show the 1500 m contour.

Size.—Reaches a SL of 180 mm (222 mm TL).

Distribution.—In Australasia, adults have been recorded from off the southern Australian coastline (Coffs Harbour, New South Wales, to Cape Naturaliste, Western Australia, including Tasmania) in depths of about 825–1260 m (Figure 6.10). Also recorded from off southern Africa and juveniles have been taken off New Zealand.

Remarks.—*O. atlanticum* is distinguished from other oreosomatids by the following characters: mostly cycloid and very deciduous scales (resulting in a very smooth body); extremely large eye (19.6–23.2% SL compared with 12.0–22.1% SL for all other oreosomatids combined); and a very pronounced horizontal ridge on the operculum.

Pseudocyttus maculatus Gilchrist, 1906
(Smooth Oreo)
Figure 6.11

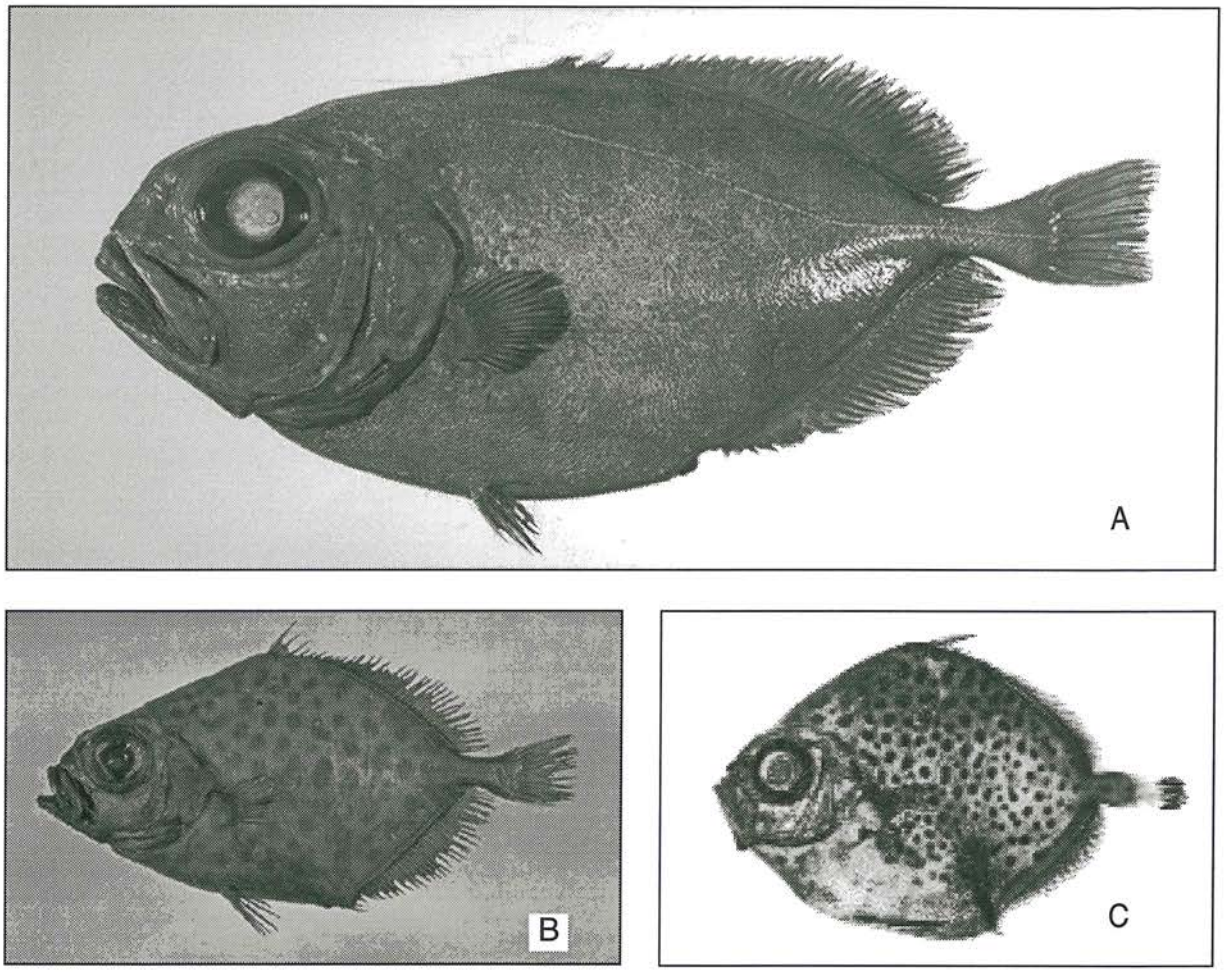


Figure 6.11. Smooth oreos, *Pseudocyttus maculatus*: A—adult, CSIRO H3972.01, 390 mm SL; B—large juvenile, CSIRO H2702.01, 179 mm SL; C—small juvenile, NMNZ P15948, 83.7 mm SL.

Holotype.—*Pseudocyttus maculatus* Gilchrist, 1906, SAM 17938, specimen lost, off Cape Point, South Africa, about 34°18'S, 18°22'E, 575–730 m, 16 Sep. 1903.

Description.—ADULTS (specimens examined 340–390 mm SL): body oval, depth 44.4–47.0% SL; predorsal profile slightly convex behind eye, predorsal length 45.8–50.0% SL; head moderately large, length 31.8–37.0% SL, width 16.5–21.1% SL; eye diameter moderately large, 13.4–16.0% SL; dorsal-fin with 39–40 spines and rays, first spine very slightly enlarged, slightly higher than second spine; second dorsal-fin spine not enlarged, slightly higher than third, height about 3.6% of SL, maximum length 0.4–0.5% SL, about 1.0 times first; anal-fin spines and rays 34–35, first spine slightly enlarged, slightly higher than second spine; 5 pelvic fin rays, pelvic-fin spine low, extending less than half the distance from pelvic-fin origin to anal opening; distance from pelvic-fin insertion to anal-fin origin 21.1–26.4% SL; 20–21 pectoral fin rays; scales mostly deciduous, those between pectoral fin and lateral line cycloid; opercles with triangular patch of cycloid scales and 8–10 very faint ridges; snout naked; head bones with faint ridges and few spinules; abdomen smooth, without protuberances, cones or warts; body light to dark bluish brown; fins mouthparts and, to a lesser extent, head darker; 41–43 vertebrae.

LARGE JUVENILES (specimens examined 169–220 mm SL): body oval to subcircular, depth 54.8–64.7% SL; predorsal profile almost straight behind eye, predorsal length 51.7–55.0% SL; head large, length 36.4–38.3% SL, width 17.3–20.1% SL; eye diameter small, 16.0–18.6% SL; first dorsal-fin spine very slightly enlarged, slightly higher than second spine; second dorsal-fin spine slightly higher than third, height about 4.8–8.9% of SL, maximum length 0.5–0.7%SL, about 0.77 times first; first anal-fin spine slightly enlarged, slightly higher than second spine; pelvic-fin spine low, extending about half way from pelvic-fin origin to anal opening; distance from pelvic insertion to anal-fin origin 22.3–26.6% SL; scales mostly deciduous, those between pectoral fin and lateral line cycloid; opercles with triangular patch of ctenoid (single ctenii) scales and 8–10 variable ridges; snout naked; head bones mostly smooth with faint ridges and few spinules; abdomen smooth, without protuberances, cones or warts; body pale bluish grey with darker roundish or oval spots (spots about equal in size to pupil diameter, fainter in larger specimens); fins and mouthparts generally darker than body.

SMALL JUVENILES (specimens examined <180 mm SL, but those measured <141 mm SL, data from James *et al.* (1988)): body nearly circular, depth 67.3–85.3% SL; predorsal profile slightly convex behind eye, predorsal length 55.7–61.2% SL; head large, length 33.0–44.9% SL; eye diameter small, 10.4–13.1% SL; first dorsal-fin spine enlarged, much higher than second spine; second dorsal-fin spine height about 8.0–10.0% of SL, about 0.71 times first; first anal-fin spine slightly enlarged; pelvic-fin spine moderately high, extending almost to anal opening; scales very adherent, those between pectoral fin and lateral line cycloid; opercles without triangular patch of radiating ridges; abdomen with several small rather indistinct protuberances; body silver grey with numreous dark blue roundish spots; fins grey, black or translucent.

Size.—Reaches 580 mm SL (679 mm TL).

Distribution.—This species is circumglobal in the Southern Ocean; juveniles have only been recorded from between 60°S and 68°S (James *et al.*, 1988). Adults are also recorded from the western and eastern South Atlantic, off southern Africa, and off

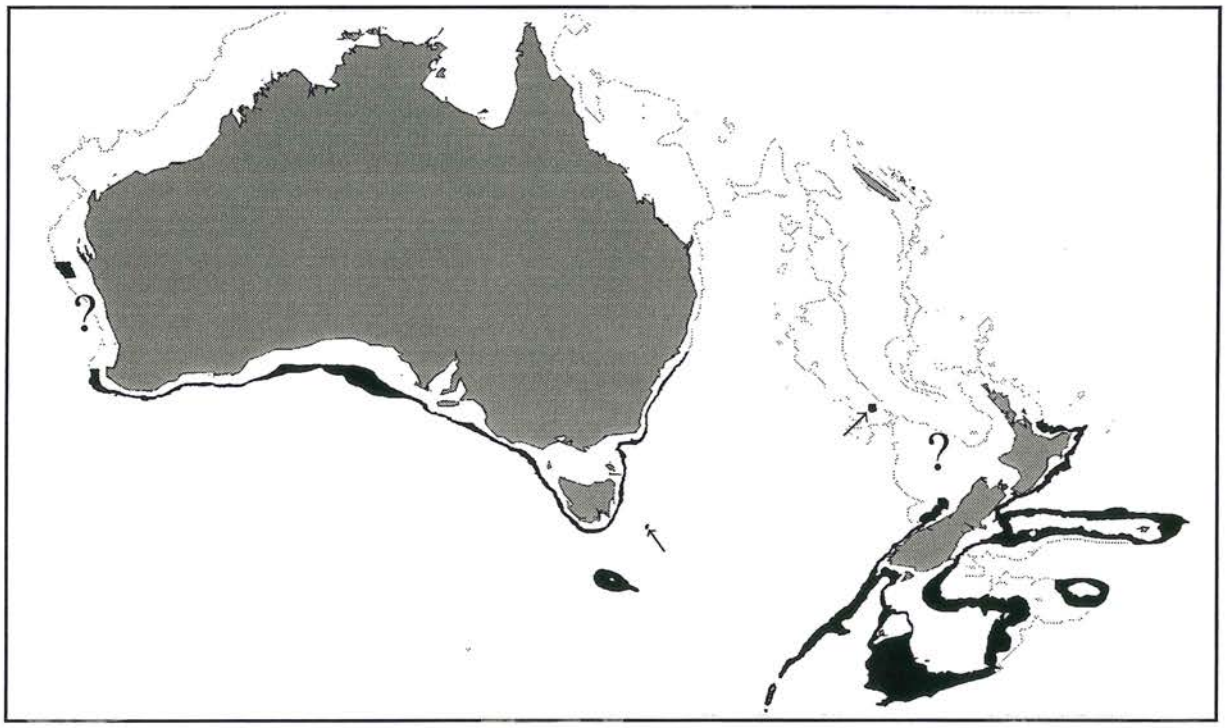


Figure 6.12. Australasian distribution of smooth oreo, *Pseudocyttus maculatus*. The dotted lines show the 1500 m contour, question marks indicate regions of suspected, though not confirmed, distribution and arrows highlight small distribution patches.

Suriname in the north Atlantic. In Australasia, it is common off southern Australia (Cape Hawke, New South Wales, to Shark Bay, Western Australia, including Tasmania) and off New Zealand (mainly in the southeast), and associated seamounts (Chatham Rise, Cascade Plateau, Lord Howe Rise, Macquarie Ridge, Puysegur Bank and South Tasman Rise) (Figure 6.12) in depths of about 650–1500 m.

Remarks.—Adult *P. maculatus* specimens differ from other adult oreosomatids in having: an oval body (body depth 44.4–47.0% SL compared with 53.4–77.6% SL in all others); the first dorsal-fin spine higher than the second (second dorsal-fin spine highest in all others); low fin spines (e.g. second dorsal-fin spine height about 3.6% SL compared with 3.9–19.8% SL in all others); and deciduous, cycloid scales (ctenoid scales in most others).

Most recent authors consider *Xenocyttus nemetoi* Abe, 1957 (recently resurrected by Miller (1993) as *P. nemetoi*) a synonym of *P. maculatus*. Further research on subantarctic oreos is needed to validate *P. nemetoi*.

Key to adult oreos of Australasia

Oreos have proven difficult to distinguish from one another, a situation not helped by incorrect photos in a recent guide to the fishes of southern Australia (Gomon *et al.*, 1994). The following key to adult oreos, together with photos of adults and juveniles on preceding pages, will assist those identifying oreos. An abbreviated key (with photos) was distributed to fishers through the "Professional Fisherman" magazine (January 1996, see Appendix 1).

The key below was compiled from a combination of characters described herein, as well as those of James (1984), James *et al.* (1988) and Paulin *et al.* (1989). Fishing zones where each species occur are included (CPF—Challenger Plateau Fishery; CRF—Chatham Rise Fishery; GABTF—Great Australian Bight Trawl Fishery; LHRF—Lord Howe Rise Fishery; MRF—Macquarie Ridge Fishery; PBF—Puysegur Bank Fishery; SEF—South East Fishery; WDWTF—Western Deep Water Trawl Fishery); bold type indicates commercial species, plain type, non-commercial species.

1a Body oval, depth 44.4–47.0% SL; first dorsal-fin spine longer than second; pelvic fin with 1 spine and 5 soft rays; opercles fully scaled, without strong bony ridge or striations. ..... *Pseudocyttus maculatus* (smooth oreo)
Fig. 6.11, **CRF, GABTF, LHRF, MRF, PBF, SEF, WDWTF**

1b Body usually rhomboidal, depth 53.1–77.6% SL; first dorsal-fin spine shorter than second; pelvic fin with 1 spine and 6 or 7 (rarely 5) soft rays; opercles not fully scaled, either with a prominent ridge or radiating striations. **2**

2a Eye huge, diameter 19.6–23.2% SL; prominent horizontal bony ridge (no radiating striations) on operculum; scales on sides of body cycloid, deciduous (body smooth). ..... *Oreosoma atlanticum* (oxeye oreo)
Fig. 6.9, **GABTF, SEF, WDWTF**

2b Eye large, diameter 14.0–21.1% SL; radiating striations (only weak horizontal ridge) on operculum; scales on most of body ctenoid (body rough). **3**

3a Predorsal profile strongly concave; abdominal plates and protuberances absent; head wide, width 17.7–23.2% SL; body light grey or light brown. **4**

3b Predorsal profile almost straight to moderately concave; prominent plates or protuberances present on abdomen (occasionally absent in large specimens of Allocyttus niger) head very wide, width 20.8–27.4% SL; body dark brown or black. **5**

4a Snout scaled; pectoral-fin rays 19–22; lachrymal narrow, width 2.2–3.6% SL; combined anal-fin spine and ray count 33–38. .... *Neocyttus rhomboidalis* (spikey oreo)
Fig. 6.5, **CPF, CRF, GABTF, LHRF, MRF, PBF, SEF, WDWTF**

4b Snout naked between lachrymal tips; pectoral fin rays 16–18; lachrymal moderately narrow, width 3.7–5.1% SL; combined anal-fin spine and ray count 31–34. ..... *Neocyttus* sp. A (rough oreo)
Fig. 6.7, **SEF, WDWTF**

5a Abdomen with 2 rows of warts (enlarged modified scales), variable in number and development; combined dorsal-fin spine and ray count 33–37; second dorsal-fin spine slightly enlarged, height 5.4–9.1% SL; pelvic-fin spine not reaching to anal opening. ..... *Allocyttus verrucosus* (warty oreo)
Fig. 6.3, **CPF, CRF, GABTF, LHRF, SEF, WDWTF**

5b Abdomen with row of scars of four scaled protuberances and a fifth scar dorsal to the posterior end of the row (scars sometimes absent in large specimens); combined dorsal-fin spine and ray count 37–41; second dorsal-fin spine greatly enlarged, height 14.4–17.7% SL; pelvic-fin spine reaching to, or extending beyond, anal opening. ..... *Allocyttus niger* (black oreo)
Fig. 6.1, **CPF, CRF, GABTF, MRF, PBF, SEF, WDWTF**

6.2. GENETIC DESCRIPTIONS

6.2.1. GENETIC VARIATION IN 'UNEXPLOITED' SAMPLE OF COMMERCIAL SPECIES

A single sample of each of the four commercial species was chosen for a base-line study of both nuclear DNA (allozyme) and mitochondrial DNA genetic variation. This examination of genetic variation in relatively unexploited stocks will enable the effects of fishing activities on genetic diversity to be monitored as the fishery for oreos continues over the coming years.

The target samples for black oreo (*Allocyttus niger*), warty oreo (*A. verrucosus*) and smooth oreo (*Pseudocyttus maculatus*) were obtained from southern Tasmania. The allozyme spikey oreo (*Neocyttus rhomboidalis*) sample came from eastern Tasmania (combination of samples ETAS 1 and ETAS 2) and the mitochondrial DNA spikey oreo sample came from western Tasmania. The planned sample sizes of 200 individuals were obtained for all the species except warty oreo, which despite repeated efforts totalled only 111 fish from this site.

For the allozyme study, 19 enzymes and muscle general proteins (as visualised following Coomassie Blue staining) were examined (Table 6.1). The total number of loci for each species varied slightly as two loci (s*MEP** and *GPI-A**), due to poor resolution, were not scored in all species, and the number of loci identified from the general protein stain varied among species. At five loci, only 24 (confidently scored) individuals were examined in some species.

Variation in mitochondrial DNA was examined using ten restriction enzymes to cut the DNA of each species (Table 6.2). These were not the same ten enzymes for each species, either because not all enzymes cut well in all species or because of poor resolution of DNA fragments after probing. Fragment sizes were determined (Appendix 3).

The spikey and smooth oreo samples displayed similar levels of allozyme variation with 13 allozyme loci displaying some variation and 10 of these being polymorphic (frequency of the most common allele less than 0.95). The warty oreo sample showed variation at nine loci and the black oreo sample at eight loci. The warty and spikey oreo samples were the most heterozygous with mean values of 0.118 and 0.115 respectively, compared to 0.101 for the smooth oreo and 0.091 for the black oreos (Table 6.3).

The relatively high mean heterozygosity for the warty oreo sample, despite fewer variable loci, arises from seven of its nine variable loci having individual heterozygosities greater than 0.400, while only three of the variable loci in the samples of the other species had heterozygosities above 0.400.

The warty oreo sample had 12 mtDNA 10-enzyme composite haplotypes with one found in 74% of the individuals examined, and six observed in only single individuals; all ten restriction enzymes showed some variation within the sample (Table 6.2). In the spikey oreo sample, two of fifteen haplotypes were common (43% and 31%), with

a third haplotype found in 11% of the individuals examined; eleven haplotypes were found in only single individuals. Only six of the ten restriction enzymes showed any variation. In the black oreo sample, six haplotypes were observed with one found in 78% of the individuals; six restriction enzymes showed variation within the sample. In the smooth oreo, six haplotypes were observed, with one found in 61% and another in 24% of the individuals examined, and only four of the restriction enzymes showed any variation within the sample.

Both haplotype diversity and nucleotide sequence diversity were highest in the spikey oreo sample (Table 6.4), followed by the smooth oreo, the warty oreo, and the black oreo. The black oreo showed the least genetic variation for both mtDNA and for allozymes.

6.2.2. GENETIC EVIDENCE OF NEW SPECIES

The rough oreo (*N.* sp. A) has been found in small numbers in commercial catches of both the black (*A. niger*) and smooth (*P. maculatus*) oreos from waters off Tasmania and Western Australia. While morphologically similar to the spikey oreo, there are diagnostic features that separate the two species, but place the rough oreo within the *Neocyttus* genus (see section 6.1). The phylogenetic relationships of the rough oreo with other members of the Oreosomatidae family are discussed in detail in section 6.3. In this section we present a more detailed comparison of the new species with both the southern hemisphere *N. rhomboidalis* and the North Atlantic *N. helgae.*

Despite small sample sizes, the rough oreo shows a higher degree of polymorphism and a higher mean heterozygosity than the other two *Neocyttus* species examined (Table 6.5) and the other oreos (Table 6.3).

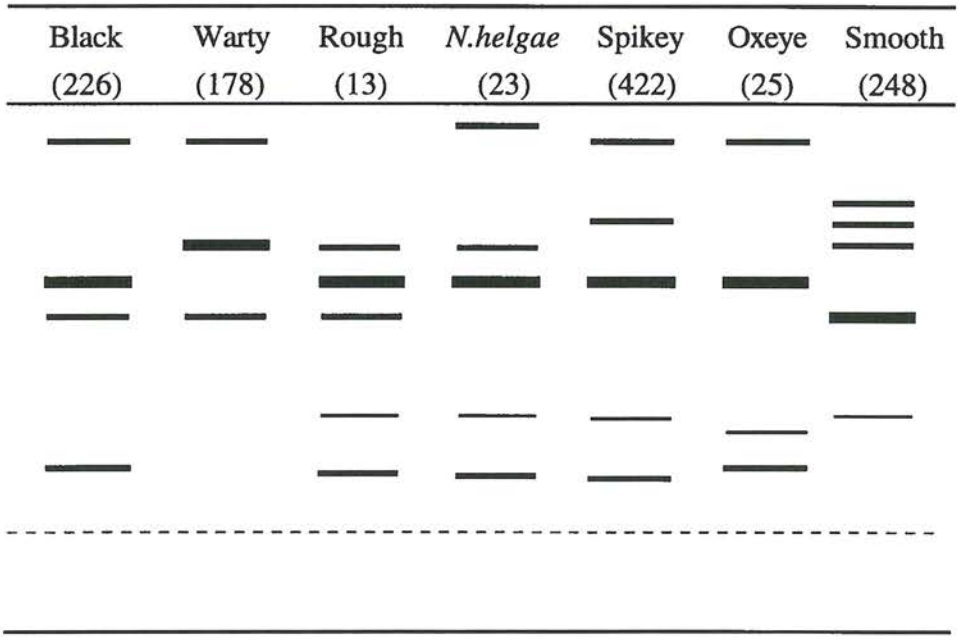
The rough oreo had a genetic identity (*I*) of 0.903 with the spikey oreo, which was similar to its identity with the black oreo (*A. niger*) (see section 6.3). Compared with the northern hemisphere *N. helgae,* the rough oreo had a genetic identity of 0.884 (spikey and *N. helgae*, I = 0.973). With the exception of distintictive general protein patterns (see Figure 6.13), there were no absolutely diagnostic loci (no shared alleles) observed between the rough and spikey oreos, but *PGDH** was operationally diagnostic. At this locus, only allele **130* was shared between the two species, but was rare in both (frequency in rough oreo, 0.042; spikey oreo, <0.001). This locus was absolutely diagnostic between the rough oreo and *N. helgae* (see Tables 6.6 and 6.11).

In addition to the *PGDH** difference, significant chi-square differences in allele frequencies were found at seven other loci between the rough and spikey oreos (*sAAT-2*, CK-A*, ESTD*, GPI-B*, LDH-1*, MPI**, and *PGM-1**) (Table 6.10). For three of these loci (*ESTD*, MPI**, and *PGM-1**), the most common alleles differed (Tables 6.6. and 6.9). There were also seven loci (excluding *PGDH**) at which allele frequencies differed between the rough oreo and *N. helgae* (*CK-A*, ESTD*, G3PDH-2*, LDH-1*, MPI*, PGM-1** and *sSOD**), and five that separated spikey oreo and *N. helgae* (*FH**,

GPI-A, GPI-B*, G3PDH-2**, and *sSOD**). The *sSOD** locus was found to separate two forms of spikey oreo based on depth of catch (see section 7.5.1 for more details), with one group found to have predominantly the **140* allele and the other the **100* allele. Each group would then differ at this locus from the rough oreo, which was found to have equal frequencies of the two alleles.

The three *Neocyttus* species have a close genetic similarity to each other and, as shown in section 6.3.3, are also similar to *A. niger,* the black oreo. Despite these close relationships, the allozyme data supports the morphological evidence that the rough oreo is a different oreosomatid species to those commonly captured in Australian waters, and is also distinct from the northern hemisphere *N. helgae.*

Figure 6.13. Banding pattern observed for each oreosomatid species with a general protein Coomassie blue stain (*PROT**). Dashed line indicates sample origin. Boldest band represents most common *CK-A** allele in each species. Numbers in brackets are number of individuals scored.



6.3. BIOCHEMICAL PHYLOGENY

The text of this section has been largely abstracted from "Genetic variation and phylogenetic relationships in seven oreo species (Teleostei, Oreosomatidae), inferred from allozyme analysis", Lowry, P.S., Elliott, N.G., Yearsley, G.K., and Ward, R.D. in press in *Fishery Bulletin* US)

6.3.1 BIOCHEMICAL PHYLOGENY: INTRODUCTION

The family Oreosomatidae (order Zeiformes) contains four genera. In a revision of oreos from the southern oceans, James *et al.* (1988) reported that, although the family is well defined and recognisable, the generic relationships are less clear: the genera *Allocyttus*, *Neocyttus* and *Oreosoma* need redefining. The fourth genus, *Pseudocyttus*, is well defined and distinguishable.

This section presents the results of an allozyme survey of the five described Australasian species (black oreo, *Allocyttus niger*, warty oreo, *A. verrucosus*; spikey oreo, *Neocyttus rhomboidalis*, oxeye oreo, *Oreosoma atlanticum*, smooth oreo, *Pseudocyttus maculatus*) and the new species (rough oreo, *Neocyttus* sp. A, Yearsley and Last unpublished) often captured with *A. niger* and *P. maculatus*. A third *Neocyttus* species, *N. helgae*, from the North Atlantic, was also examined.

Oreosomatids not included in this study are the North Pacific *Allocyttus folletti* , the southern Atlantic and Indian Ocean *Allocyttus guineensis*, and the Indian Ocean *Neocyttus acanthorhyncus*. Another member of the family, the Southern Ocean *Pseudocyttus nemotoi*, was recently resurrected by Miller (1993) but its validity has not been confirmed.

The intrarelationships of zeiforms have not been discussed in the literature, making outgroup selection for this phylogenetic study difficult. Many authors consider the beryciforms to be more primitive than the zeiforms, and closely related to them (e.g. Greenwood *et al.*, 1966). Zehren (1979) found the Berycidae to be more primitive than the remaining beryciform families and, thus, a berycid may be a suitable outgroup. However, Rosen (1984) dramatically changed the placement of the zeiforms, including them in the Order Tetraodontiformes, with the Caproidae as the sister group to all other tetraodontiforms (the caproids' placement within the Zeiformes was questioned by others (Tighe and Keene, 1984)). A caproid may therefore be a suitable outgroup. Furthermore, Rosen placed the zeids immediately before the oreosomatids in his new Division Zeomorphi. He used "acanthurids plus chaetodontids" to establish character polarities. Consequently, a zeid or an acanthurid are also possible outgroups. In the absence of caproid specimens, three outgroups were selected for analysis: the berycid *Beryx splendens* Lowe 1833 (alfonsino), the zeid *Cyttus australis* (Richardson 1843) (silver dory), and the acanthurid *Naso tuberosus* Lacépède 1802 (humphead unicornfish).

Twenty-seven loci were examined in the oreos and the outgroups, and allele frequencies determined (Table 6.11). However, the locus *GPI–A** was not included in the phylogenetic analyses because of poor resolution in three species (black, rough and smooth oreos). The mean sample sizes per locus for the seven oreo species had a wide range (from 14 to 598, Table 6.7), primarily because polymorphic loci for the four main commercial species (*A. niger, A. verrucosus, N. rhomboidalis* and *P. maculatus*) were examined in large numbers for the stock delineation studies (see Section 7).

6.3.2 BIOCHEMICAL PHYLOGENY: RESULTS

The percentage of variable loci (presence of more than one allele at a locus), of the 26 loci scored in the seven oreosomatids, ranged from 19.2% (5 loci) for oxeye (*O. atlanticum*) to 65.4% (17 loci) for spikey (*N. rhomboidalis*) (Tables 6.7 and 6.11). Despite a relatively low sample size, the rough oreo, *N.* sp. A, had the highest proportion of polymorphic loci (a locus was considered polymorphic when the frequency of the most common allele was less than 0.95) with 46.2% (12 loci); the four commercial species (*A. niger, A. verrucosus, N. rhomboidalis* and *P. maculatus*) had either 26.9% or 34.6% polymorphism (7 or 9 polymorphic loci). The mean heterozygosity per locus ranged from 0.083 in *O. atlanticum* to 0.181 in *N.* sp.; in the four commercial species it ranged from 0.105 to 0.127 (Table 6.7).

O. atlanticum was the most divergent of the oreosomatids (Table 6.8). Its average genetic identity (Nei 1978; 0 indicates complete dissimilarity and 1 complete similarity) to the other species was 0.371 (range 0.313 to 0.426 for 26 loci). The two most similar species were *N. rhomboidalis* and *N. helgae*, with a high genetic identity of 0.973. The third *Neocyttus* species, *N.* sp. A, had a relatively lower identity to the other two *Neocyttus* species: 0.903 with *N. rhomboidalis* and 0.884 with *N. helgae*. The two *Allocyttus* species had a genetic identity of only 0.695.

The three outgroup species were very divergent, from both the oreosomatids and each other (Table 6.8). The acanthurid *N. tuberosus* diverged most from the oreosomatids, with an average genetic identity of 0.112 (range 0.085 to 0.180, from 23 loci). *C. australis* had a mean identity to the oreosomatids of 0.171 (range 0.108 to 0.199, 26 loci) and *B. splendens* a mean identity of 0.164 (range 0.115 to 0.222, 22 loci).

In the acanthurid *N. tuberosus,* 16 of the 23 scorable loci were diagnostic (no shared alleles with any oreosomatid), in the zeid *C. australis* , 15 of 26 loci and in the berycid *B. splendens,* 15 of 22 loci were diagnostic (Table 6.11). Comparing the oreosomatids with one another, *O. atlanticum* had eleven diagnostic loci, *P. maculatus* three, *A. verrucosus* two, while the other four species had only the muscle protein patterns as diagnostic (Table 6.9, Figure 6.13). However, when the seven oreosomatids were compared pair-wise, each pair (except *N. rhomboidalis* with either *N.* sp. A or *N. helgae*) had at least one and up to fourteen diagnostic allozyme loci, other than the general protein difference (Table 6.10). With the addition of between 4 and 13 loci

showing significant allele frequency differentiation ($P<0.05$, with Bonferroni adjustment for multiple tests) (Table 6.10), even the closely related *N. rhomboidalis* and *N. helgae* were found to differ at five loci (*FH*, GPI-A*, GPI-B*, G3PDH-2** and *sSOD**) and *N. rhomboidalis* and *N.* sp. A at eight loci (*sAAT-2*, CK-A*, ESTD*, GPI-B*, LDH-1*, MPI*, PGDH** and *PGM-1**). The locus *PGDH** was diagnostic between *N.* sp. A and *N. helgae,* with allele frequency differences at a further seven loci (*CK-A*, ESTD*, G3PDH-2*, LDH-1*, MPI*, PGM-1** and *sSOD**). *O. atlanticum* differed from the other six species at between 17 and 22 loci, in addition to the general protein difference.

Two loci – *AK** and *GAPDH-2** – were invariant across all seven oreosomatid species, but only *GAPDH-2** differed in all three outgroup species; *AK** was different only in *C. australis*. These loci are consistent with a monophyletic origin of the oreosomatids. Three loci (*GAPDH-1**, *mIDHP** and *sMDH-2**) were monomorphic for the same allele in six of the seven oreo species, with *O. atlanticum* fixed for alternative alleles; these putative synapomorphies indicate these six species are probably monophyletic.

It is therefore not surprising to find that *O. atlanticum* was clearly separated from the other oreosomatid species on the phenogram constructed by the UPGMA method from Nei's (1978) unbiased genetic distances (Figure 6.14). Branching order and significance of the branching nodes did not differ with the choice of outgroup. The three *Neocyttus* species and *A. niger* formed a distinct cluster. There was a very close association of the Southern Hemisphere *N. rhomboidalis* and the Northern Hemisphere *N. helgae.*

The phylogenetic tree constructed by the distance-Wagner procedure from Rogers' (1972) distances, rooted by the outgroup *C. australis*, also showed the divergence of *O. atlanticum* from the other oreosomatids (Figure 6.15). While the closeness of *N. rhomboidalis* and *N. helgae* was maintained, and again the two *Allocyttus* species were not grouped together, *P. maculatus* was found to be grouped with *A. niger* and *N.* sp. A. A similar tree was produced with *N. tuberosus* as the outgroup, whereas the tree produced with *B. splendens* as the outgroup resembled those from the cluster analyses (with *P. maculatus* divergent from the *Neocyttus* and *Allocyttus* species); a similar tree was produced when applying all three outgroups together.

Figure 6.14. UPGMA phenogram constructed from Nei's (1978) unbiased genetic distance. Open boxes represent standard error (Nei, 1987) of the branch nodes.

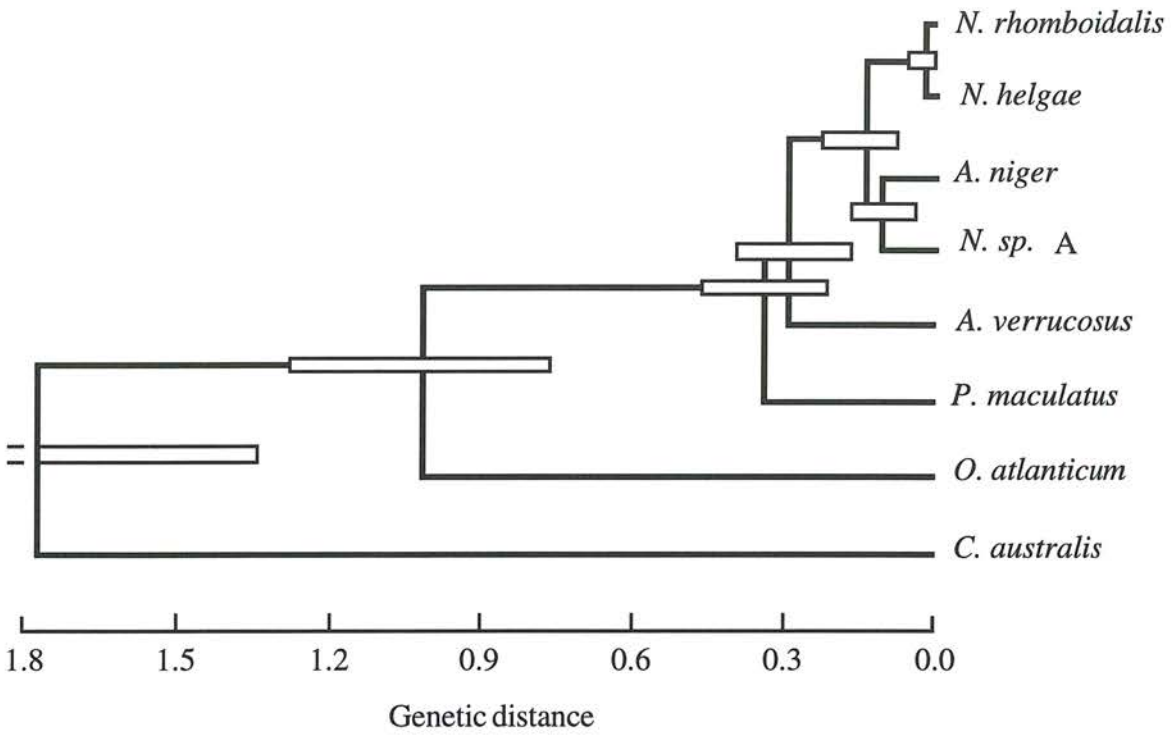
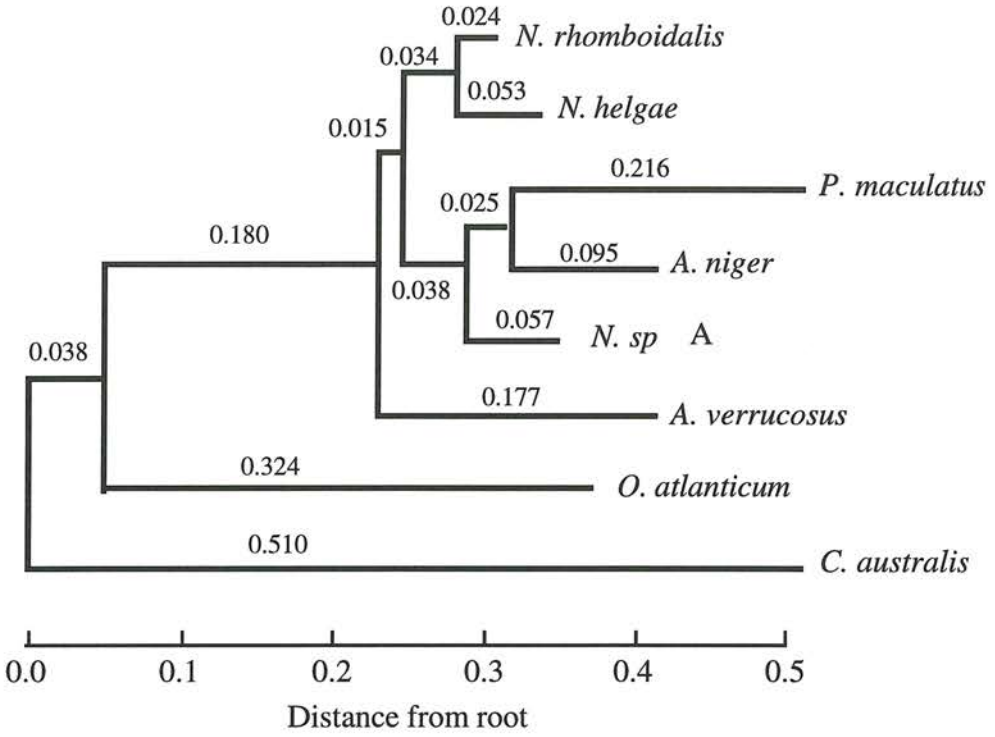


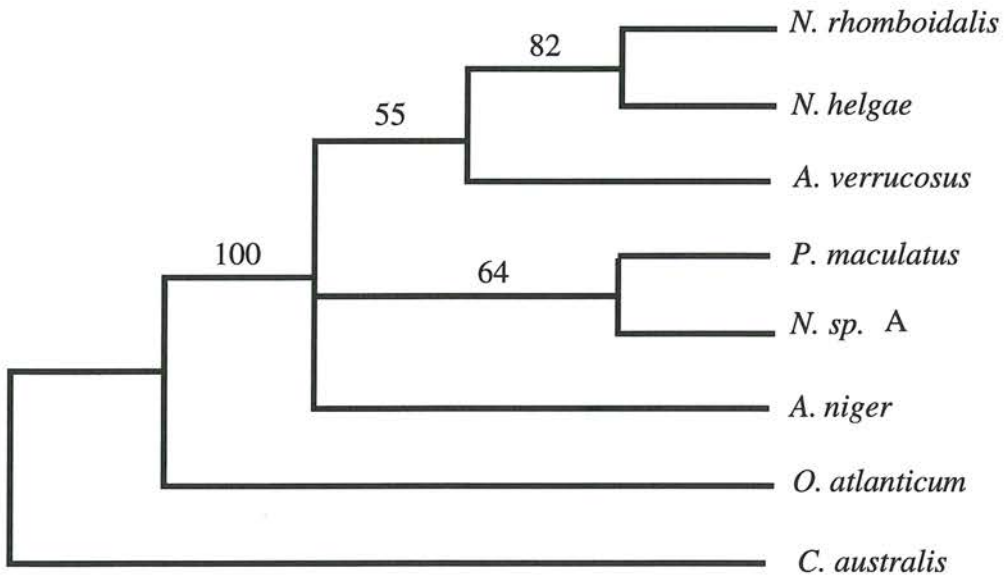
Figure 6.15. Tree constructed from Rogers' distance by the distance-Wagner procedure. Numbers represent relative branch lengths.



Cladistic analysis (PAUP) with all three outgroup species together produced 55 most parsimonious trees, all of which showed the divergence of *O. atlanticum* from the other members of the family, but failed to define any structure for the other six species. Analysis with *C. australis* as the outgroup produced eleven most parsimonious trees of 52 units in length, all again showing the divergence of *O. atlanticum* , but this time defining some structure to the other species. The 50% majority-rule consensus tree is shown in Figure 6.16. The most significant difference in this analysis from the two phenetic analyses is the reversal of the positions of the two *Allocyttus* species. In the cladistic analysis *A. niger* is separated from the other species, while *A. verrucosus* grouped with either *P. maculatus* and *N.* sp. A or the other two *Neocyttus* species. Applying a topological constraint to the search (enforcing predetermined groupings and keeping only those trees that satisfy the constraints) for the three *Neocyttus* species or the two *Allocyttus* species produced shortest trees only one step longer than the most parsimonious under no-constraint searches. A search for near-optimal trees with lengths of 53 units produced 56 trees, with 98% confirming the branch separation of *O. atlanticum*, and 71% supporting the separation of *N. rhomboidalis* and *N. helgae* from the other four species, among which the branching points could not be resolved.

The zeids appear to be the most likely sister family to the oreosomatids after the cladistic analyses. Neither analysis with the berycid or the acanthurid produced shortest trees that resembled in any way the trees produced from the phenetic analyses nor the cladistic analyses with either all three outgroups or *C. australis* alone. *N. tuberosus* as the outgroup resulted in a single shortest tree (49 units) with *A.*

Figure 6.16. The 50% majority-rule consensus tree of the eleven shortest trees produced by PAUP analysis. Numbers represent percentage consensus measures.



verrucosus as the most divergent oreosomatid and *O. atlanticum* grouped next to the *N. rhomboidalis* and *N. helgae* cluster. Four shortest trees (42 units) resulted from the analysis with *B. splendens*, all of which, while confirming the divergence of *O. atlanticum*, resulted in *N. rhomboidalis* and *N. helgae* diverging independently from the other four species.

6.3.3 BIOCHEMICAL PHYLOGENY: DISCUSSION

The mean heterozygosity per locus for the seven oreosomatid species, over the 26 loci scored in common, ranged from 8.3% to 18.1% (Table 6.7). These are considerably higher than the mean figure of 5.1% for 195 species of marine and freshwater fish (Ward *et al., 1992*) and 5.5% for 106 species of marine teleosts (Smith and Fujio 1982). Three of the seven species had mean heterozygosity values (12.1% to 18.1%) that exceeded the highest value of 11.7% reported by Ward *et al.* (1994b) from comparisons of genetic diversity among populations of 57 species of marine fish. This value was shown by two species, *Fundulus heteroclitus* (Linnaeus 1766) (15 loci, Ropson *et al., 1990*) and *Hoplostethus atlanticus* (22 loci, Smith 1986), although subsequent studies of additional loci in *H. atlanticus* raised its mean heterozygosity to 13.0% (Elliott and Ward 1992).

It is clear that oreosomatids have higher heterozygosities than most teleosts. Interestingly, both oreosomatids and the similarly variable *H. atlanticus* are deepwater (500–1200 m) species. Elliott and Ward (1992) speculated that for *H. atlanticus*, the high heterozygosity may reflect its large (pre-exploitation) population sizes and (assuming that deepwater species have been less severely affected by glaciations than shallow water species) a possible lack of severe bottlenecks in their recent evolutionary past.

Mitochondrial DNA nucleotide sequence diversities per target sample ranged from an average of about 0.0032 (spikey oreos), through 0.0021 (smooth oreos) and 0.0017 (warty oreos) to 0.0012 (black oreos). Comparable figures for other teleosts are: jackass morwong, 0.0046 (nine restriction enzymes, Grewe *et al.*, 1994), orange roughy, 0.0018 (nine restriction enzymes, Elliott *et al.*, 1994), yellowfin tuna, 0.0036 (eight restriction enzymes, Ward *et al.*, 1994a). The oreos have a little less mtDNA variation than most other species assayed thus far in our laboratory.

As adults, *Pseudocyttus* is the most morphologically distinct oreosomatid genus (James *et al., 1988*). Its distinguishing characters include the first dorsal-fin spine being longer than the second (vice versa in other species), a pelvic fin with only five rays (usually six or seven in other species) and 40–43 vertebrae (34–41 in other species). However, as juveniles, the genus *Oreosoma* is the most distinctive with prominent cones over the body. Most other juvenile oreosomatids have 'warts' or protuberances (such structures are absent in at least *N. rhomboidalis*) but none are quite so pronounced or bizarre as in *O. atlanticum*. Our genetic study confirms the uniqueness of *O. atlanticum*, which has a very low genetic identity (0.371) to the other oreosomatid species – substantially less than the corresponding mean (0.650) of *P. maculatus* to

the other oreos. Morphologically, *O. atlanticum* can be distinguished as an adult by a very large eye (eye diameter 52–60% of head length) and a prominent horizontal ridge on the operculum.

James *et al.* (1988) suggested that further study may synonymise the northern hemisphere *N. helgae* with the southern hemisphere *N. rhomboidalis*. Our allozyme data suggest that, while these two taxa are indeed very closely related (genetic identity I = 0.973 for 26 loci and I = 0.966 for 27 loci including *GPI-A**), their distinctive muscle protein patterns, not included in the genetic identity values, are consistent with their being separate species. Of the four non-*CK-A** protein bands, two appear to be fixed differently for the two species. Classical morphological techniques confirm their taxonomic separation (Yearsley and Last unpublished). However, the amount of genetic differentiation between these two species is only a little greater than that between samples of *H. atlanticus* taken from the same two areas (North Atlantic and off southern Australia) (Elliott *et al., 1994*). Eleven polymorphic loci were screened in the *H. atlanticus* comparison, with just three loci showing significant heterogeneity, and giving a genetic identity of 0.990 (unpublished data)

The new species *N.* sp. A, infrequently captured with *P. maculatus* and *A. niger* in southern Australian waters, and morphologically similar to *N. rhomboidalis*, showed quite a high degree of genetic similarity to the other two *Neocyttus* species (I = 0.903 with *N. rhomboidalis* and 0.884 with *N. helgae*). However, it was genetically distinct from them at several loci (Table 6.10), and numerous meristic and morphological characters (Yearsley and Last unpublished, and see section 6.1) confirm that it is a separate species. While it clustered with *A. niger* (I = 0.903) in the two phenetic trees constructed from the genetic distance data, in the cladistic analyses it grouped more often with *P. maculatus*. However, classical taxonomic techniques suggest a close association with *Neocyttus* species, particularly the western Indian Ocean *N. acanthorhynchus* (Yearsley and Last unpublished).

The two *Allocyttus* species were found to be genetically quite distinct from one another (I = 0.695), with no evidence from either phenetic or cladistic analyses that they comprised an exclusive monophyletic group. James *et al.* (1988) gave no justification for placing *A. niger* in *Allocyttus*. However, they drew attention to problems with generic diagnoses of the oreosomatids. *Allocyttus*, as it currently stands, but excluding *A. niger* (i.e. *A. verrucosus*, *A. guineensis* and *A. folletti*), may be a natural grouping, with *A. niger* more akin to, but probably not congeneric with, *Neocyttus*.

While the branch node for *O. atlanticum* is clearly resolved as ancestral to the remaining oreosomatids, the phenetic and cladistic analyses could not unambiguously resolve all the internal nodes for the remaining species. There is strong evidence for a branch node separating *N. rhomboidalis* and *N. helgae* from the other four species, but no evidence supporting two species in *Allocyttus*.

Table 6.1. Allele frequency of each allele observed within the target sample for each of the four commercial oreo species. *H* = Nei's (1978) unbiased heterozygosity estimate. N = number of individuals scored, # = locus not scored due to poor resolution.

Locus	Allele	Black oreo (STas)	Warty oreo (STas)	Spikey oreo (ETas)	Smooth oreo (STas)
*sAAT–1**	110	–	1.000	0.254	–
	100	1.000	–	0.746	0.962
	80	–	–	–	0.038
	H	*0.000*	*0.000*	*0.380*	*0.073*
	N	24	24	203	199
*sAAT–2**	120	–	–	0.002	–
	100	1.000	0.991	0.993	0.988
	80	–	0.005	0.005	0.007
	60	–	0.005	–	0.005
	H	*0.000*	*0.018*	*0.014*	*0.025*
	N	202	111	211	200
*mAAT**	100	–	–	0.002	–
	0	–	–	0.013	–
	–100	1.000	1.000	0.870	0.950
	–200	–	–	0.113	0.050
	–250	–	–	0.002	–
	H	*0.000*	*0.000*	*0.230*	*0.095*
	N	202	111	274	200
*ADH**	125	–	–	–	1.000
	100	1.000	1.000	1.000	–
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200
*AK**	100	1.000	1.000	1.000	1.000
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	24	24	200
*CK–A**	110	–	0.861	–	–
	100	0.866	0.139	0.951	–
	90	0.134	–	0.049	1.000
	H	*0.232*	*0.240*	*0.094*	*0.000*
	N	202	126	274	200
*ESTD**	115	1.000	1.000	–	1.000
	100	–	–	1.000	–
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200

Table 6.1. continued

Locus	Allele	Black oreo (STas)	Warty oreo (STas)	Spikey oreo (ETas)	Smooth oreo (STas)
*FH**	120	0.005	–	–	–
	115	–	0.008	–	0.007
	113	–	–	0.005	–
	110	–	–	–	0.023
	100	0.990	0.726	0.985	0.837
	80	0.005	0.266	0.009	0.132
	H	*0.020*	*0.403*	*0.029*	*0.281*
	N	201	126	274	200
*GAPDH–1**	100	1.000	1.000	1.000	1.000
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	24	24	24	24
*GAPDH–2**	100	1.000	1.000	1.000	1.000
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	24	24	24	24
*GPI–A**	150		0.012	–	
	140		0.004	–	
	130		0.238	0.009	
	125		0.012	0.018	
	115		0.714	0.315	
	100		0.012	0.628	
	97		0.008	–	
	90		–	0.011	
	85		–	0.018	
	H		*0.434*	*0.506*	
	N	#	126	273	#
*GPI–B**	140	–	0.004	0.004	–
	120	–	0.080	–	–
	100	1.000	0.532	0.551	1.000
	80	–	0.380	0.445	–
	60	–	0.004	–	–
	H	*0.000*	*0.568*	*0.499*	*0.000*
	N	202	125	274	200
*G3PDH–2**	165	–	–	0.002	–
	130	0.128	0.015	0.051	–
	100	0.555	0.550	0.906	–
	75	0.317	0.431	0.041	–
	70	–	–	–	1.000
	65	–	0.005	–	–
	H	*0.577*	*0.515*	*0.175*	*0.000*
	N	191	101	266	200

Table 6.1. continued

Locus	Allele	Black oreo (STas)	Warty oreo (STas)	Spikey oreo (ETas)	Smooth oreo (STas)
*sIDHP**	100	1.000	1.000	1.000	1.000
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200
*mIDHP**	100	1.000	1.000	1.000	1.000
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200
*LDH–C**	100	1.000	1.000	1.000	0.810
	85	–	–	–	0.190
	H	*0.000*	*0.000*	*0.000*	*0.309*
	N	202	111	211	200
*LDH–1**	100	1.000	1.000	1.000	0.775
	40	–	–	–	0.225
	H	*0.000*	*0.000*	*0.000*	*0.350*
	N	202	111	211	200
*LDH–2**	100	0.062	1.000	1.000	1.000
	50	0.938	–	–	–
	H	*0.116*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200
*sMDH–1**	110	–	1.000	–	–
	100	1.000	–	1.000	1.000
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200
*sMDH–2**	100	1.000	1.000	1.000	1.000
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200
*sMEP**	100	1.000	1.000		1.000
	H	*0.000*	*0.000*		*0.000*
	N	202	111	#	200
*MPI**	110	–	0.374	0.041	–
	100	–	0.626	0.754	0.144
	90	1.000	–	0.204	0.856
	80	–	–	0.002	–
	H	*0.000*	*0.470*	*0.389*	*0.247*
	N	202	99	270	206
*PEP1–1**	100	1.000	1.000	1.000	–
	90	–	–	–	0.997
	80	–	–	–	0.003
	H	*0.000*	*0.000*	*0.000*	*0.005*
	N	202	111	211	199

Table 6.1. continued

Locus	Allele	Black oreo (STas)	Warty oreo (STas)	Spikey oreo (ETas)	Smooth oreo (STas)
*PEP2**	105	–	1.000	–	–
	100	1.000	–	1.000	0.502
	85	–	–	–	0.498
	80	–	–	–	–
	H	*0.000*	*0.000*	*0.000*	*0.501*
	N	202	24	211	217
*PGDH**	120	–	–	0.009	–
	110	0.642	–	0.173	–
	100	0.294	1.000	0.812	0.935
	90	–	–	0.005	0.035
	85	–	–	–	0.030
	75	0.063	–	–	–
	H	*0.498*	*0.000*	*0.311*	*0.124*
	N	197	111	274	200
*PGM–1**	110	–	–	0.002	–
	105	–	0.130	0.069	–
	100	0.015	0.710	0.627	–
	95	0.715	0.136	0.259	0.020
	90	0.249	0.025	0.037	0.629
	85	0.021	–	0.006	0.020
	80	–	–	–	0.330
	H	*0.427*	*0.463*	*0.535*	*0.495*
	N	195	81	268	197
*PGM–2**	130	–	0.004	–	–
	125	–	–	0.002	–
	120	0.005	0.262	0.030	0.002
	100	0.598	0.714	0.917	0.910
	80	0.279	0.016	0.046	0.087
	65	0.103	0.004	0.006	–
	50	0.015	–	–	–
	H	*0.555*	*0.423*	*0.156*	*0.165*
	N	199	124	271	214
*sSOD**	180	–	–	–	0.382
	140	0.187	1.000	0.143	0.618
	100	0.813	–	0.857	–
	H	*0.305*	*0.000*	*0.246*	*0.474*
	N	198	111	272	200
General protein	no. loci	3	2	4	4
	H	*0.000*	*0.000*	*0.000*	*0.000*
	N	202	111	211	200

Table 6.2. Haplotype frequency of each 10-restriction enzyme haplotype observed within the target samples for each of the four commercial oreo species. N = number of individuals scored. Fragment patterns for each restriction enzyme haplotype are given in Appendix 3.

Black oreo (STas N = 96).
Restriction enzyme order:
Ava I, *Bst*E II, *Dra* I, *Eco*R I, *Hind* III, *Kpn* I, *Pst* I, *Pvu* II, *Sty* I, *Xba* I.

Haplotype	Frequency
ADAEBCAAAA	0.781
ADAEBAAAAA	0.094
ADAEBCABAA	0.063
ADAEFCAAAA	0.042
AFAEBCAAAA	0.010
CDBEBCAAAA	0.010

Warty oreo (STas N = 85).
Restriction enzyme order:
Afl II, *Apa*L I, *Ava* I, *Ban* I, *Bgl* I, *Eco*R I, *Eco*R V, *Hind* III, *Pvu* II, *Xba* I.

Haplotype	Frequency
AABAAFAGCA	0.741
AABABFAGCA	0.059
ABBAAFAGCA	0.059
AABAACAGCA	0.024
AABBBFAGCA	0.024
CABACFAGCA	0.024
AAAAAFAGCA	0.012
AABAAEAGCA	0.012
AABAAFAGCB	0.012
AABAAFBGCA	0.012
AABABFBGCA	0.012
BABAAFAGCA	0.012

Spikey oreo (W Tas N = 90)
Restriction enzyme order:
Afl II, *Apa* I, *Ava* I, *Bst*E II, *Eco*R I, *Hind* III, *Pst* I, *Pvu* II, *Sma* I, *Xba* I.

Haplotype	Frequency
AAAAAAAAAA	0.433
AABAAAAAAA	0.311
ABAAAAAAAA	0.111
AABAABAAAA	0.022
ABBAAAAAAA	0.011
ACAAAAAAAA	0.011
AABAAGAAAA	0.011
AACAAAAAAA	0.011
ABABAAAAAA	0.011
ABBBAAAAAA	0.011
AAABAAAAAA	0.011
AABBAAAAAA	0.011
AACAAAAAAA	0.011
ABAABAAAAA	0.011
BABAAAAAAA	0.011

Smooth oreo (STas N = 95)
Restriction enzyme order:
Apa I, *Ava* I, *Bst*E II, *Dra* I, *Eco*R I, *Hind* III, *Pst* I, *Pvu* II, *Sty* I, *Xba* I.

Haplotype	Frequency
HACCCDAADA	0.611
HACCCEAADA	0.242
HACCDDAADA	0.116
HADCDDAADA	0.011
HDCCDDAADA	0.011
HGECCDAADA	0.011

Table 6.3. Summary of genetic variability statistics for the allozyme loci examined in the 'target' samples of the four commercial oreo species.

	Black (STas)	Warty (STas)	Spikey (ETas)	Smooth (STas)
Number loci examined	30	30	31	31
Mean sample size per locus	183.2	97.2	214.2	189.7
Mean heterozygosity	0.091 ± 0.034	0.118 ± 0.037	0.115 ± 0.320	0.101 ± 0.030
Mean number alleles per locus	1.53 ± 0.19	1.87 ± 0.29	2.16 ± 0.30	1.65 ± 0.160
% loci polymorphic (0.95)	23.33	26.67	32.26	32.26
% loci variable	26.67	30.00	41.94	41.94

Table 6.4. Summary of genetic variability statistics for the mtDNA genome in the 'target' samples of the four commercial oreo species.

	Black (STas)	Warty (STas)	Spikey (WTas)	Smooth (STas)
Number of restriction enzymes	10	10	10	10
Sample size	96	85	90	95
Haplotype diversity	0.379	0.452	0.709	0.560
Nucleotide diversity	0.0012[a]	0.0017	0.0032	0.0021[a]

[a] Excluding data from *Sty* I

Table 6.5. Comparison of genetic statistical information on 26 loci scored for the three *Neocyttus* species. Means and standard errors are presented.

	Mean sample size per locus	Mean no. alleles per locus	% loci variable	% loci polymorphic (0.95)	Mean heterozygosity
N. sp. A	14.0 ± 16.7	1.7 ± 0.1	53.8	46.2	0.181 ± 0.041
N. rhomboidalis	597.6 ± 63.1	2.5 ± 0.3	65.4	34.6	0.127 ± 0.037
N. helgae	28.7 ± 1.1	1.7 ± 0.2	38.5	30.8	0.093 ± 0.032

Table 6.6. Frequencies of major alleles at loci for which significant differences exist between the three *Neocyttus* species. ns = not scored due to poor resolution.

Locus	Allele	*N. sp. A* (Rough)	*N. rhomboidalis* (Spikey)	*N. helgae*
*sAAT-2**	100	0.875	0.996	0.986
*CK-A**	100	0.731	0.952	1.000
*ESTD**	115	0.856	-	-
	100	0.154	0.998	1.000
*FH**	100	0.962	0.982	0.939
*GPI-A**	115	ns	0.338	0.031
	110		-	0.484
	100		0.610	0.469
*GPI-B**	100	0.692	0.550	0.849
	80	0.269	0.446	0.121
*G3PDH-2**	100	0.846	0.900	0.355
	75	0.154	0.046	0.548
*LDH-2**	100	0.594	0.999	1.000
	40	0.406	0.001	-
*MPI**	100	0.318	0.779	0.804
	90	0.682	0.170	0.125
*PGDH**	160	0.750	-	-
	150	0.208	-	-
	100	-	0.803	1.000
*PGM-1**	100	-	0.609	0.517
	95	0.433	0.242	0.450
	90	0.500	0.043	0.033
*SOD**	140	0.500	0.487	0.057
	100	0.500	0.513	0.929

Table 6.7. Comparison of genetic statistical information on in each species. A locus is considered variable when more than one allele present, and polymorphic when the frequency of the most common allele is 0.95 or less. Mean and standard errors are presented. Mean heterozygosity per locus is Nei's (1978) unbiased estimate. Data are for 26 loci scored in all species except BS (22 loci) and NT (23 loci) (see Table 6.11).

Species	Mean sample size per locus	Mean no. alleles per locus	Percentage of loci variable	polymorphic	Mean heterozygosity
AN	228.1±16.7	1.6±0.2	30.8	26.9	0.105±0.038
AV	237.7±40.9	1.8±0.3	30.8	26.9	0.116±0.039
NA	14.0±0.3	1.7±0.1	53.8	46.2	0.181±0.041
NH	28.7±1.1	1.7±0.2	38.5	30.8	0.093±0.032
NR	597.6±63.1	2.5±0.3	65.4	34.6	0.127±0.037
OA	22.0±1.0	1.3±0.2	19.2	15.4	0.083±0.041
PM	297.8±22.0	1.8±0.2	50.0	34.6	0.121±0.034
BS	5.8±0.1	1.2±0.1	9.1	9.1	0.061±0.042
CA	5.8±0.2	1.3±0.1	23.1	23.1	0.062±0.025
NT	2.0±0.0	1.1±0.1	8.7	8.7	0.051±0.035

Table 6.8. Pairwise comparison of Nei's (1978) unbiased genetic identity (above diagonal) and genetic distance (below diagonal) between species for 26 loci, except for BS (22 loci) and NT (23 loci).

Species	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
AN	–	0.695	0.903	0.852	0.841	0.342	0.738	0.118	0.199	0.095
AV	0.364	–	0.773	0. 761	0.788	0.313	0.659	0.183	0.169	0.180
NA	0.102	0.257	–	0.884	0.903	0.402	0.764	0.184	0.177	0.108
NH	0.160	0.273	0.123	–	0.973	0.426	0.711	0.174	0.180	0.085
NR	0.173	0.238	0.102	0.027	–	0.422	0.711	0.152	0.174	0.086
OA	1.073	1.161	0.913	0.853	0.864	–	0.319	0.222	0.108	0.128
PM	0.304	0.417	0.269	0.341	0.342	1.143	–	0.115	0.191	0.100
BS	2.138	1.700	1.694	1.749	1.885	1.505	2.159	–	0.068	0.095*
CA	1.614	1.780	1.734	1.714	1.748	2.227	1.653	2.689	–	0.042
NT	2.353	1.714	2.229	2.465	2.456	2.057	2.303	2.355*	3.168	–

(* 21 loci common to both species)

Table 6.9. Alleles present at each locus for the seven oreosomatid species. Alleles are given as letters in alphabetic order according to their anodal mobility (see Table 6.11). Diagnostic alleles (not shared with another species) are shown in bold; most common allele in variable loci is underlined. - = locus not scored (see text).

	Locus	AN	AV	NA	NH	NR	OA	PM
1	*sAAT-1**	*c*	*b*	*bc*	*bc*	*bc*	***a***	***cd***
2	*sAAT-2**	*c*	*cef*	*ac*	*ac*	***ab***c***e***	***d***	*cef*
3	*mAAT**	*c*	*c*	*cf*	*cf*	***abcfg***	*c*	*cf*
4	*ADH**	*b*	*b*	*b*	*b*	*b*	***ce***	***a***
5	*AK**	*a*	*a*	*a*	*a*	*a*	*a*	*a*
6	*CK-A**	*bc*	*ab*	*ab*	*b*	*abcd*	*b*	*c*
7	*ESTD**	*c*	*c*	*cd*	*d*	***de***	*d*	*c*
8	*FH**	***a***e***g***	*beg****b***	*eg*	*deg*	***c***e***g***	*g*	*bdeg*
9	*GAPDH-1**	*b*	*b*	*b*	*b*	*b*	***c***	*b*
10	*GAPDH-2**	*a*	*a*	*a*	*a*	*a*	*a*	*a*
11	*GPI-B**	*f*	*ac****f****ik*	*fik*	***df****i*	*afik*	*f*	*f*
12	*G3PDH-2**	*def*	*def****b***	*ef*	***b****ef*	***a****def*	***c***	***g***
13	*sIDHP**	*d*	*d*	*d*	*d*	***df***	***a***	*d*
14	*mIDHP**	*b*	*b*	*b*	*b*	*b*	***a***	*b*
15	*LDH-C**	*a*	*a*	*a*	*a*	*ab*	*b*	*ab*
16	*LDH-1**	*a*	*a*	*ab*	*a*	*ab*	***c***	*ab*
17	*LDH-2**	*a****b***	*a*	*a*	*a*	*a*	*a*	*a*
18	*sMDH-1**	*d*	***c***	*d*	*d*	*d*	***b***	*d*
19	*sMDH-2**	*b*	*b*	*b*	*b*	*b*	***a***	*b*
20	*MPI**	*c*	*abc*	*bc*	*abc*	*abcd*	*bc*	*bc*
21	*PEP1-1**	*a*	*a*	*a*	*a*	*a*	*a*	***bd***
22	*PEP2**	*b*	***a***	*b*	*b*	*bc*	*b*	*bc*
23	*PGDH**	*fh****k***	*h*	***ab****c*	*h*	*cdfhi*	***e***	*hi****j***
24	*PGM-1**	*defg*	*cdef*	*efg*	*def*	***abc****defg*	*gh****i***	*efgh*
25	*PGM-2**	*cdfg****i***	***ac****dfg*	*cd*	*cdf*	***b****cdfg*	*cdfg*	*cdf*
26	*sSOD**	*bd*	*b*	*bd*	*abd*	*bd*	*abe*	*ab*
27	*GPI-A**	-	***ab****cdegh****i***	-	*cefg*	*cdeg****ijk***	*g*	-
	No. diagnostic loci	0	2	0	0	0	11	3

Table 6.10. Pairwise comparison of oreo species. Above the diagonal: diagnostic loci (no shared alleles), including general protein (PROT); below the diagonal: loci with shared alleles but significant differences in allele frequencies (chi-square test, $P<0.05$ with Bonferroni adjustment), including the *GPI-A** locus. Total numbers are in bold and each locus is identified by the reference number shown in Table 6.9.

	AN	**AV**	**NA**	**NH**	**NR**	**OA**	**PM**
AN		**4** 1,18,22 PROT	**2** 23, PROT	**2** 7, PROT	**2** 7,PROT	**14** 1,2,4, 7,9 12,13,14,15 16,18,19,23 PROT	**4** 4,12,21 PROT
AV	**10** 6,8,11,12 17,20,23 24,25,26		**4** 18,22,23 PROT	**4** 7,18,22 PROT	**4** 7,18,22 PROT	**15** 1,2,4,7,9,12 13,14,15,16 18,19,22,23 PROT	**8** 1,4,6,12 18,21,22 PROT
NA	**9** 2,6,7,11 16,17,20 25,26	**8** 1,2,6,7 16,20,24 26		**2** 23, PROT	**1** PROT	**13** 1,2,4,9,12,13 14,15,16,18, 19,23, PROT	**6** 4,6,12,21 23,PROT
NH	**9** 3,11,12 17,20,23 24,25,26	**9** 1,6,8,11 12,20,24 26,*GPI-A**	**7** 6,7,12,16 20,24,26		**1** PROT	**14** 1,2,4,9,12,13, 14,15,16,18, 19,23,24, PROT	**6** 4,6,7,12 21,PROT
NR	**11** 1,3,6,11 12,17,20 23,24,25 26	**11** 1,3,6,8 11,12,20 23,25,26 *GPI-A**	**8** 2,6,7,11, 16,20,23 24	**5** 8,11,12,26 *GPI-A**		**12** 1,2,4,9,12,13, 14,16,18,19, 23,PROT	**5** 4,7,12,21 PROT
OA	**6** 8,17,20 24,25,26	**8** 6,8,11,20 24,25,26 *GPI-A**	**6** 6,7,8,11, 24,26	**4** 8,20,26 *GPI-A**	**8** 8,11,15,20 24,25,26 *GPI-A**		**15** 1,2,4,6,7,9 12,13,14,16 18,19,21,23 PROT
PM	**12** 3,6,8,15 16,17,20 22,23,24 25,26	**10** 3,8,11,15 16,20,23 24,25,26	**8** 1,2,7,11 15,22,24 26	**9** 1,11,15 16,20,22 24,25,26	**13** 1,3,6,8 11,15,16 20,22,23 24,25,26	**7** 8,15,20,22, 24,25,26	

7. STOCK STRUCTURE

7.1. INTRODUCTION

What is a stock? Different individuals have their own ideas on what constitutes a stock, and many definitions exist in the literature. A stock is often defined by fisheries managers as a group of fish existing in a specified area or exploited by a particular method. This is a pragmatic definition, and one which may pay little heed to the underlying population structure of that species. Consequently, derived yield estimates may be erroneous or misleading. A scientifically more supportable definition is that a stock is "an intraspecific group of randomly mating individuals with temporal and spatial integrity" (Ihssen *et al.*, 1981). Different stocks of fish, as so defined, are likely to have different biomasses and are likely to respond differently to exploitation; if boundaries between them can be drawn, and if other relevant information is available, then an optimal harvesting strategy for each stock can be devised. However, in practise it is enormously difficult to decide from existing data where boundaries are to be drawn: data are generally limited and often fraught with interpretation problems; marine systems pose particular problems in that the habitable environment is often continuous (unlike, for example, lakes or streams) with marked opportunities for gene flow by larval and/or adult movement.

Various methods have been applied in attempts to delineate stock boundaries. These include genetics, tagging, parasite loads, otolith microchemistry, morphology, ecology (e.g. location of spawning sites), and all have their attendant advantages and disadvantages. No single approach provides sufficient information to unequivocally resolve such issues.

Genetic information is powerful when it provides clear evidence of genetic heterogeneity between areas, because this is generally most reasonably ascribed to reproductive isolation and stock separation, but genetic homogeneity can be maintained by high or quite low levels of gene flow. The former result thus provides useful information for management, the latter is less useful. It should be pointed out that the null hypothesis under test is that samples come from a single panimctic population, and that a failure to reject this hypothesis (i.e no detected heterogeneity) does not prove the null hypothesis to be correct, rather that the data fail to reject it. Under such circumstances, the null hypothesis may be correct, or it may be that additional data would lead to its rejection.

Tagging data show that a fish has moved from A to B, and the recent development of archival tags now permits an assessment of where the fish went on its journey from A to B. However, movement of fish does not necessarily equate to gene flow, since the fish may not spawn in area B. Furthermore, tagging is relatively simple (if expensive and time-consuming) for large pelagic fish, but far more difficult for deep water demersal fish. For species such as oreos and orange roughy, it has not so far proved possible to devise a practical tagging program.

Studies based on techniques such as morphological and otolith microchemical analysis generally have interpretational difficulties, in that the relevant contributions of genetic and environmental variation are unknown. Thus, any observed differences between fish from different areas may be ascribable either to genetic differentiation or to environmental differences. Environmental variation may be totally irrelevant to stock delineation issues, as fish that have experienced different environments may in fact belong to the same freely interbreeding stock. Some of these approaches, such as meristic counts (e.g. of fin rays or vertebral numbers) and the more recent development of otolith primordium analysis, are more powerful than simple morphometric comparisons or analyses of whole otoliths, since the former are generally laid down, irreversibly, early in development (although the timing varies for different meristic traits, see Lindsey, 1988), while the latter are integrated over the entire life history of the fish. However, inter-year environmental changes could affect meristic counts and otolith primordium chemistry, meaning that differences in the distributions of such characters between regions might reflect different year-class distributions rather than true stock differentiation. This is a particularly severe problem in long-lived fish like oreos, which cannot be aged to a particular year class, making it impossible to compare identical year classes. Even if it were possible to age oreos to the correct birth year, the large spread of ages within a sample (perhaps up to 100 different cohorts) would mean that extremely large sample sizes would be necessary to sample adequately a single cohort. Nonetheless, we were interested to assess levels of variation for meristic characters in these species, and to see if the data thus collected supported genetic evidence of stock structuring.

Since no one approach to delineating stock structures provides a definitive answer, we utilised a combined genetic and meristic approach to enhance the power of our analyses.

Several genetic techniques are capable of revealing genetic variation that can be examined for spatial differentiation. We chose to use two techniques: allozyme analysis and mitochondrial DNA analysis. Mitochondrial DNA analysis may have greater resolving power for sub-population discrimination than allozyme analysis (Avise, 1987; Ward and Grewe, 1994), because restriction enzyme analysis of DNA allows variability at synonymous and non-coding sites to be detected, because mtDNA evolves at 5-10 times the rate of single-copy nuclear DNA (Brown *et al.*, 1979), and because mtDNA is only inherited from females and thus has an effective population size smaller than nuclear DNA making it more sensitive to bottleneck effects (Birky *et al.*, 1989). However, the disadvantage of mtDNA is that it is a non-recombining small molecule, effectively behaving as just one single character, whereas there are very large numbers of independent allozyme loci that can be examined. We have chosen to use both allozyme and mtDNA approaches for increased power.

We opted to study a number of meristic traits: counts of various fin rays and spines, gill rakers, pyloric caeca, and lateral line scales. Fin ray elements are laid down during embryonic and early larval development, and are then fixed in number, but in at least some teleosts the full complement of gill rakers, pyloric caeca and scales may not

become apparent until the juvenile phase. Indeed, in some teleosts, gill rakers may be added throughout life. The general ontogeny of such traits has been reviewed by Lindsey (1988), but nothing is known of their development in oreos.

Samples of the four major commercial species of oreo (black, smooth, warty and spikey) were collected from various regions of Australasia and analysed for genetic (allozyme and mitochondrial DNA) and morphological variation. Unfortunately, and despite our best endeavours, only a few samples of some of the species could be collected. Where possible, all fish in a sample were examined for polymorphic allozymes, and a subset (usually 24) examined for those enzymes that appeared to be monomorphic or nearly so (frequency of the most common allele>0.95) in the study of the target sample of that species. The extra work and expense involved in mtDNA analysis meant that sample sizes for this character were smaller than for the allozyme analyses. For black oreos, all ten restriction enzymes were used. For the warty, smooth and spikey oreos, just the two most polymorphic were used. This chapter discusses these genetic and morphological results in relation to the possible stock structure of each species.

7.2. BLACK OREO, *ALLOCYTTUS NIGER*.

A large and well preserved sample from southern Tasmania was collected and analysed for all characters: allozymes, mtDNA, and meristics.

A large sample was also collected from New Zealand. Nine of these were whole fish which were examined for allozyme, mtDNA and meristic variation. Tissue samples were obtained from another 90 fish from the same collection, and analysed for allozymes and mtDNA.

A sample of fish collected from the South Tasman Rise a year before this project started was also examined. This sample had been stored at -20^{o}C, but on thawing out were found to be in a poor condition. They could not be reliably scored for liver-specific allozymes, for mtDNA, or for meristic characters. We were only able to collect good data from the four polymorphic allozyme loci that were scorable from muscle tissue.

Ten whole fish from Western Australia were also collected, but they had been poorly stored at some time post-capture and could not be reliably scored for any genetic traits; meristic data were however satisfactory.

7.2.1. BLACK OREO: GENETIC DATA

Only two samples, one from southern Tasmania (the "target" sample, n=c.200) and one from New Zealand (n=c.90), could be analysed for the complete suite of allozyme characters. Eight allozyme loci out of the 27 scored showed genetic variation (Table 7.1), although this was very limited for two loci (*FH** and *LDH-2**). No significant

deviations from Hardy-Weinberg equilibrium at any locus in either sample were detected. The average heterozygosity per locus was 0.101 ± 0.037 in the southern Tasmania sample and 0.100 ± 0.037 in the New Zealand sample (Table 7.2).

With respect to the mtDNA analysis, 96 fish from southern Tasmania and 76 fish from New Zealand were examined (Table 7.3). Eight (*Ava* I, *Bst* EII, *Dra* I, *Eco* RI, *Hind* II, *Kpn* I, *Pvu* II, *Sty* I) of the ten restriction enzymes detected variation, two (*Pst* I, *Xba* I) did not. Fragment sizes were determined (Appendix 3). A total of 11 composite haplotypes was found, but one haplotype was observed in about 75% of individuals. Six haplotypes were each found in single individuals. There was therefore relatively little mtDNA variation detected in this species, with haplotype diversities being a low 0.379 and 0.474 in the southern Tasmanian and New Zealand populations respectively, and sequence diversities 0.0012 and 0.0015 respectively.

Despite the examination of allozymes in about 200 fish from southern Tasmania and 90 from New Zealand, chi-square analysis revealed no significant differences in allele frequencies at any locus (Table 7.4.a). The observed G_{ST} values were very low, ranging from 0.007 to less than 0.001 (Table 7.4.a), meaning that less than 1% (0.7% to less than 0.1%) of the total genetic variation at each locus could be ascribed to population differences. In fact, none of these values were significantly greater than the values that could be ascribed to sampling variance alone ($G_{ST.null}$), so there was no evidence from the G_{ST} analysis for significant population differentiation. The mtDNA analyses for heterogeneity showed significant haplotype differentiation using the chi-square analysis but not the G_{ST} analysis (P=0.034 and 0.223 respectively, Table 7.4.a). Deleting haplotype ADAEBCABAA, found in six southern Tasmanian but no New Zealand fish, gives a non-significant chi-square result (P=0.146). The G_{ST} analysis showed that about 1% of the variance in haplotype frequencies could be ascribed to population variation, but this was not significantly greater than that attributable to sampling factors alone (0.6%).

Finally, the sample of around 40 fish from the South Tasman Rise that could be scored only for four of the polymorphic allozymes (and not at all for mtDNA) showed no statistically significant differences from the southern Tasmania and New Zealand samples (Table 7.4.b).

7.2.2. BLACK OREO: MERISTIC DATA

Meristic counts were made on black oreo from three samples, Western Australia (WA), southern Tasmania (STAS) and New Zealand (NZ) (Table 7.5).

Counts of pectoral fin rays on the left and right side of the body did not differ significantly (n = 69, mean difference between left and right = 0.043, SD = 0.580, P = 0.536). Similarly, the total number of gill rakers did not differ between the left and right sides of the body (n = 71, mean difference (L-R) = 0.282, SD = 1.578; P = 0.137).

There was no significant difference observed between the three samples for the counts of dorsal fin spines and rays (CD χ^2 = 11.602, P = 0.207) and anal fin spines

and rays (AC χ^2 = 9.580, P = 0.345), nor for the total number of gill rakers on either side of the body (LTGR χ^2 = 29.558, P = 0.026 (not significant after Bonferroni adjustment for multiple tests); RTGR χ^2 = 18.490, P = 0.190).

The three samples were significantly differentiated (P = 0.002) for lateral line scale counts (ranging from 88 to 116 per individual), the STAS individuals having a significantly higher mean count (102.31±4.90) than those from WA (96.80±5.77) or NZ (97.78±5.33) (STAS/WA, P = 0.002; STAS/NZ, P = 0.015; WA/NZ, P = 0.676). Sample sizes for NZ and WA were very small (9 and 10 respectively). While there was no significant correlation between lateral line scale count and fish length in the single sample with n>20 (STAS, n = 45, Table 7.6), the STAS fish (318±30mm) were on average larger (see Table 5.1) than fish from NZ (293±44mm) or WA (297±40mm), possibly accounting for some or all of the difference in scale count.

The number of pyloric caeca in a black oreo ranged from 9 to 16 (Table 7.5), with the means of the three samples varying significantly (P = 0.002). The NZ fish had a significantly higher mean value (13.33±0.87) than those from STAS (11.61±1.41) or WA (12.11±1.62) (NZ/STAS P <0.001; NZ/WA P = 0.021; WA/STAS P = 0.869), but sample sizes for NZ and WA were very small (9 each). There was no significant correlation between pyloric caeca and fish length in the single sample with n>20 (STAS, n=203, Table 7.6).

7.2.3. BLACK OREO: CONCLUSIONS

The null hypothesis states that the samples that were analysed constituted a single stock. No significant allozyme differences between the southern Tasmanian, New Zealand and South Tasman Rise samples were observed. There was some weak evidence for mtDNA differentiation between the Tasmanian and New Zealand samples (the South Tasman Rise sample could not be tested for this character), but this was only apparent from one of the two statistical tests applied, and then was only just statistically significant (P = 0.034). We recommend the examination of mtDNA of a further 100 individuals taken from each of the Australian and New Zealand sides of the Tasman Sea. Furthermore, we also recommend the analysis of additional fish from Western Australia, although the minimal genetic differentiation of populations across the Tasman Sea suggests that it is unlikely that Western Australia fish would be markedly differentiated from Tasmanian fish, given the continuity of habitable slope between the latter two regions.

There was no evidence for any significant difference in dorsal- and anal-fin meristic counts, nor in gill raker counts, between fish from Western Australia, southern Tasmania and New Zealand. However, with respect to lateral line scales, fish from southern Tasmania had higher mean counts than those from Western Australia and New Zealand, and with respect to pyloric caeca, fish from New Zealand had higher counts than fish from southern Tasmania and Western Australia, which were not significantly different. Thus, despite the small sample sizes, the three samples all differed from one another in one of these two meristic characters. This provides

evidence against the null hypothesis of a single unit stock, and suggests instead the existence of (at least) three unit stocks: Western Australia, southern Tasmania, and New Zealand. While meristic differentiation by itself is weak evidence of stock structuring, given possible environmental influences and the possibility of different year-class mixtures in different samples, the observation of mtDNA, pyloric caeca and lateral line scale count differentiation of New Zealand fish from southern Tasmanian fish does provide evidence that these two areas constitute different stocks. Whether Western Australia fish constitute a third stock is debatable: more samples from this region need to be analysed to determine if they are likely to be distinct from southern Tasmanian fish.

7.3. SMOOTH OREO, *PSEUDOCYTTUS MACULATUS*

Three large samples of smooth oreos were collected; one from Western Australia, one from southern Tasmania, and one from New Zealand. They were analysed for allozymes and mtDNA. Meristic counts were also made on about 50 fish from each of the southern Tasmanian and Western Australian samples, and nine whole specimens from New Zealand were also examined.

A small sample (n=15) of smooth oreo from Lord Howe Rise was also obtained. These were analysed for mtDNA and for meristic variation, but allozyme degradation in these fish meant that the allozyme loci could not be assessed. In addition pyloric caeca counts were made on fish collected from western Tasmania (WTAS) and the South Tasman Rise (STR).

7.3.1. SMOOTH OREO: GENETIC DATA

Three large samples of smooth oreo were examined for the complete suite of allozyme characters: Western Australia (n = c.100), southern Tasmania (the "target" sample, n = c.220), and New Zealand (n = c.100). Thirteen out of the 29 allozyme loci scored showed genetic variation (Table 7.7), although this was very limited for five loci (*mAAT*, sAAT-1*, sAAT-2*, PEP1-1*, PGDH**). No significant deviations from Hardy-Weinberg equilibrium at any locus were detected. The average heterozygosity per locus was very similar to the black oreo: 0.110 ± 0.032 for Western Australia, 0.110 ± 0.032 for Tasmania, and 0.101± 0.030 for New Zealand (Table 7.8).

With respect to the mtDNA analysis, just over 90 fish from each of Western Australia, southern Tasmania and New Zealand were examined, together with 15 fish from Lord Howe Rise (Table 7.9). Two (*Eco* RI, *Hind* III) of the ten restriction enzymes were used to detect variation. Fragment sizes were determined (Appendix 3). Three composite haplotypes were found. One haplotype was found in 50-70% of individuals, with a second haplotype in 13-35%. A third haplotype was found in 12-20% of individuals. Haplotype diversity was higher than in black oreos, at around 0.6 for each sample. Nucleotide sequence diversity averaged 0.009.

Despite the examination of about 200 fish from southern Tasmania and nearly 100 fish from each of Western Australia and New Zealand, no statistically significant differences in allele frequencies at any allozyme locus were apparent (Table 7.10.a). The only locus that showed any suggestion of significant differentiation was *MPI** (chi-square, P = 0.048; G_{ST}, P = 0.057), but this loses significance following the application of Bonferroni procedures for multiple tests (13 loci, in this case). Neither the chi-square nor G_{ST} analysis showed significant mtDNA haplotype differentiation (P = 0.450 and 0.368, respectively). There was no significant mtDNA differentiation when the small Lord Howe Rise sample was added to the mtDNA analysis (Table 7.10.b)

7.3.2. SMOOTH OREO: MERISTIC DATA

Meristic counts were made on smooth oreo from four samples: Western Australia (WA), southern Tasmania (STAS), Lord Howe Rise (LHR) and New Zealand (NZ) (Table 7.11). In addition pyloric caeca counts were made on fish collected from western Tasmania (WTAS) and the South Tasman Rise (STR).

Counts of pectoral-fin rays on the left and right side of the body did not differ significantly (n = 134, mean difference between left and right = 0.030, SD = 0.714, P = 0.629). Similarly, the total number of gill rakers did not differ between the left and right sides of the body (n = 133, mean difference (L-R) = 0.075, SD = 1.369; P= 0.528).

There was no significant difference between the four samples for the counts of dorsal-fin spines and rays (CD χ^2 = 16.067, P = 0.367) and anal fin spines and rays (AC χ^2 = 8.681, P = 0.956), nor for the total number of gill rakers on the right side of the body (RTGR χ^2 = 29.786, P = 0.200). Significant differentiation was observed for the total number of gill rakers on the left side (LTGR χ^2 = 41.204, P = 0.007), possibly due to the small sample size from New Zealand. No significant pairwise comparisons of the four samples for LTGR were apparent.

Lateral line scale counts could not be taken reliably from the New Zealand sample, so for this character only three samples of smooth oreo (southern Tasmania, Western Australia, and Lord Howe Rise) could be compared. Individual fish counts ranged from 98 to 133, with significant differentiation between the values of the three samples (P < 0.001). The WA individuals had significantly higher counts (117.19±7.79) than those from STAS (108.15±6.36) and LHR (107.86±5.42) (WA/STAS, P < 0.001; WA/LHR, P < 0.001; STAS/LHR P = 0.894). In neither of the two samples with n>20 (STAS, n = 40; WA, n = 51) was there a significant correlation between lateral line scale count and length; indeed, the (non-significant) correlations were negative (Table 7.12). Thus while the WA fish were larger than those from STAS (Table 7.12, P <0.001), this is unlikely to be the explanation of their increased scale count.

The number of pyloric caeca present in a smooth oreo was markedly different to the other three oreo species examined. Values for the other oreos ranged between 8-16 (black oreo), 7-11 (warty oreo) and 8-14 (spikey oreo), but for smooth oreo ranged between 75 and 299. Values for the two samples from western Tasmania and from

South Tasman Rise, not given in Table 7.11, are as follows: WTAS, n = 7, mean = 223.57, min. = 180, max. = 262, SD = 26.73; STR, n = 52, mean = 182.52, min. = 106, max. = 266, SD = 40.71. There was significant differentiation between the six samples (P = 0.005), which was associated with the small WTAS sample having a higher mean value than the other samples. Removing the WTAS sample from the analysis results in a non-significant comparison between the other samples. Four samples had n>20; all showed a positive correlation between pyloric caeca count and fish length (Table 7.12), although only one of these (STAS Rise, with P=0.003) remained significant following Bonferroni correction for four multiple tests.

7.3.3. SMOOTH OREO: CONCLUSIONS

There was no evidence of any allozyme or mtDNA differentiation of the large samples of fish taken from Western Australia, southern Tasmania, and New Zealand. Thus the null hypothesis that smooth oreo from these three widely separated areas form a single panmictic population cannot be rejected. Lord Howe Rise fish, which could only be examined for mtDNA variation, were also not separable from these three samples.

The meristic data, in the form of the lateral line scale counts (but no other character examined), distinguished the Western Australia samples from the STAS and LHR samples (too few whole New Zealand fish were available for this analysis). This is the only evidence which points towards some stock separation of smooth oreos, and the standard caveat must be raised that this might well reflect differences in year-class mixtures between sites rather than true stock differentiation.

7.4. WARTY OREO: *ALLOCYTTUS VERRUCOSUS*

A total of ten samples was collected. Five of these were from Western Australia, one from the Great Australian Bight, one from southern Tasmania, one from New South Wales, one from Lord Howe Rise, and a small sample from South Africa.

Four of these collections were in good condition on reaching the Hobart laboratory: Western Australia IV, southern Tasmania, New South Wales, and South Africa. These samples were analysed for the complete range of allozyme, mtDNA, and meristic characters. The Western Australia IV and southern Tasmania samples were large, the New South Wales sample medium, and the South Africa sample small.

Large samples were also obtained from the Great Australian Bight and Lord Howe Rise, but these were not in good condition on arrival and because of liver degradation could not be assessed for liver-specific allozymes. However, they were examined for the muscle-specific allozymes and about 24 fish from each sample were also screened for mtDNA variation. They were also examined meristically.

The Western Australia I, II, III and V samples were similarly degraded on arrival. They were only assessed for muscle-specific allozyme polymorphisms and not at all for

mtDNA. Pyloric caeca were counted on fish from all Western Australia samples, and individuals from WA II and WA III were included with WA IV in the full meristic analysis.

7.4.1 WARTY OREO: GENETIC DATA

Two large samples of warty oreo were collected in good condition for genetic analysis. The southern Tasmanian sample was designated as the "target" sample, although its size (n = 126) was smaller than the intended target size of 200. The second good sample was from Western Australia (WA IV, n = c.150). Small samples of good condition fish from New South Wales (n = 32) and South Africa (n=11) were also examined. Twenty five loci were analysed in these four samples, of which nine were variable (Table 7.13). The average heterozygosity per locus for these samples was around 0.130 to 0.140 (Table 7.14), slightly higher than either black or smooth oreos. No significant deviations from Hardy-Weinberg equilibria were noted.

With respect to the mtDNA examination, two of the ten restriction enzymes revealed haplotype variation (*Bgl* I, *Eco* RI), but this variation was very limited (Table 7.15). Fragment sizes were determined (Appendix 3). Six composite haplotypes were found in the six samples, but two of these were only found once. A single haplotype predominated with a frequency of 80% to 97%.

The first set of stock structure analyses (Table 7.16.a) only considered the three "good" Australian collections (WAIV, NSW and STAS). Seven of the nine variable allozyme loci showed no indications of geographic heterogeneity. One locus, *MPI**, showed highly significant heterogeneity in allele frequencies ($P<0.001$ with both chi-square and G_{ST} analyses); this heterogeneity remained significant even after Bonferroni corrections to probability values to allow for the nine tests. However, allele *MPI*100* was always the most common allele followed by allele *MPI*110*. Thus the allele frequency differentiation, while significant, was not extensive, and only about 5% of the variation at this locus could be ascribed to among population variation (G_{ST} of 0.061 minus $G_{ST\cdot null}$ of 0.007 ± 0.007). Comparing these populations pairwise indicates that the heterogeneity arises from the southern Tasmanian sample (Table 7.17). A second locus, *PGM-1**, showed indications of significant heterogeneity (P = 0.032 and 0.014 following the chi-square and G_{ST} analyses respectively), but this became non-significant following probability correction for multiple tests. No significant heterogeneity in mtDNA haplotype frequencies was detected following chi-square analysis (P = 0.810) or G_{ST} analysis (P = 0.246). Haplotype diversity in these three populations ranges from 0.063 in NSW to 0.276 in STAS. Nucleotide sequence diversities appear to be similarly variable, ranging from 0.001 to 0.006.

The second set of analyses considered these three "good" Australian samples along with the "good" (but small) South African sample (Table 7.16.b). The South African sample had a similar mean heterozygosity per locus (0.148) as the Australian samples (Table 7.14). Of the nine variable loci, *MPI** again showed highly significant differentiation following the chi-square analysis ($P<0.001$) but not the G_{ST} analysis

(P=0.103). This latter result was unexpected, given the highly significant result from the three Australian samples. It appears to arise from a statistical quirk: the G_{ST} value is derived from the allele frequencies of the contributing samples regardless of population size, while the mean bootstrapped G_{ST} value, $G_{ST.null}$, does reflect population size and the small South African sample had the effect of considerably increasing the standard error of the G_{ST} values. In this instance, the chi-square probability value is the more credible, and again it is the southern Tasmanian sample that is the source of the heterogeneity (Table 7.17). The lack of significant deviation for *MPI** of the South African sample compared with the Australian samples is perhaps not surprising given the small South African sample size (n = 6). The mtDNA analyses again both showed non-significant results (chi-square P = 0.842, $G_{ST}P$ = 0.357). The common Australian haplotype was also the most common South African haplotype.

In addition to the "good" sample, samples from other collections from Western Australia (WA I, WA II, WA III and WA V), the Great Australian Bight, and Lord Howe Rise were also examined. Livers of these samples had degraded, but the five muscle-specific allozyme polymorphisms were scored. None of these showed evidence of population differentiation (Table 7.16.c). MtDNA variation was scored in the Great Australian Bight and Lord Howe Rise samples, but no significant differentiation from these and the other scored samples was observed.

7.4.2. WARTY OREO: MERISTIC DATA

Six samples of warty oreos (Western Australia, Great Australian Bight, southern Tasmania, New South Wales, Lord Howe Rise, and South Africa) were examined meristically (Table 7.18). However, the South African sample was not in good condition and only 1-3 fish could be analysed for most meristic characters. The exception was pyloric caeca count, where 10 South African fish were measured. In the following analyses, the South African fish are only included in the pyloric caeca analysis.

Counts of pectoral-fin rays on the left and right side of the body did not differ significantly (n = 393, mean difference between left and right = 0.059, SD = 0.622, P = 0.063). Similarly, the total number of gill rakers did not differ between the left and right sides of the body (n = 382, mean difference (L-R) = -0.055, SD = 1.447; P = 0.458).

There was no significant difference observed between the five samples for the counts of the total number of gill rakers on either side of the body (LTGR χ^2 = 20.462, P = 0.658; RTGR χ^2 = 34.658, P = 0.165), nor for the anal-fin spines and rays (AC χ^2 = 28.857, P = 0.028, not significant after Bonferroni adjustment for multiple tests). However, there was significant differentiation for the dorsal fin spines and rays (CD χ^2 = 50.315, P = 0.007). Pairwise comparisons of the five samples (Table 7.19) reveals that this difference is associated with the LHR sample, which had a lower mean value than the other samples. This difference was particularly striking for the LHR/WA comparison. This is unlikely to reflect size differences, as although the LHR sample

had a smaller mean size (190±44 mm) than the WA sample (212±30 mm), there was no significant correlation between CD and size in the large WA IV sample (n = 152, r = 0.019, $P = 0.816$).

As there was no difference between the WA and GAB samples they were combined and compared with the nearest geographic sample STAS ($\chi^2 = 3.858$ $P = 0.423$). These three samples showed no differences and so were combined and compared to the NSW sample. Following Bonferroni adjustment, the chi-square value ($\chi^2 = 14.129$, $P = 0.043$) was not significant and so the four samples (WA, GAB, STAS and NSW) were combined. The chi-square comparison of this combined sample and the LHR sample was significant ($\chi^2 = 27.382$, $P < 0.001$).

Lateral line counts ranged from 74 to 105 and were significantly differentiated ($P < 0.001$), with the WA individuals having significantly higher counts (mean of 90.30, the next highest being LHR with a mean of 87.73) than those from the other four samples (WA/GAB, $P < 0.001$; WA/STAS, $P < 0.001$; WA/NSW, $P < 0.001$; WA/LHR, $P = 0.002$). The only other significant pairwise comparison was between LHR and GAB ($P = 0.001$), with the LHR sample having the higher counts (means of 87.73 and 84.52 respectively). There was evidence of a (weak) positive correlation between lateral line scale count and fish length (Table 7.20): all five samples with n>20 showed a positive correlation; three of these had probabilities just less than 0.05, and a fourth had a probability of 0.063. Bonferroni corrections for multiple tests would make these results non-significant, but they are certainly suggestive. Furthermore, the WA sample, with the highest mean count, had the greatest mean fish length of any sample except that from NSW (where n was only 27), and LHR had a higher mean fish size than GAB. Thus, the apparent differences in lateral line scale counts might well reflect differences in mean fish size rather than true size-corrected differences in scale count.

The number of pyloric caeca in warty oreos ranged between 6 and 11 (Table 7.18). The ANOVA result for the six samples (which included South Africa) was not significant ($P = 0.045$) given the adjustment for multiple tests, and no pairwise comparisons were significant. Four of the five correlations between pyloric caeca count and fish length were positive (Table 7.20), and two of these had probabilities less than 5% (but greater than 1%). However, these results are non-significant following Bonferroni corrections, and the largest sample (WA, n=266) showed a very small correlation (0.067, $P = 0.273$). Therefore, there is little evidence for a relationship between pyloric caeca count and fish length.

7.4.3. WARTY OREO: CONCLUSIONS

The genetic analysis revealed one locus, *MPI**, that differentiated the southern Tasmanian sample from Western Australia (WA IV) and New South Wales samples. Unfortunately, this was a liver-specific locus and due to liver degradation could not be scored in other samples from Western Australia nor in samples from the Great Australian Bight and Lord Howe Rise. No other allozyme polymorphisms showed any

significant differentiation among Australian samples. Mitochondrial DNA variation was low in this species and did not differentiate among the three samples.

With respect to the meristic characters, dorsal-fin ray counts separated the Lord Howe Rise sample from Western Australia, Great Australian Bight, southern Tasmania, and New South Wales, and lateral line scale counts distinguished the combined Western Australia sample from other samples, and also separated Lord Howe Rise from the Great Australian Bight. Thus, on the combined meristic evidence, Lord Howe Rise could be considered as one stock, Western Australia as another stock, Great Australian Bight as a third stock, and southern Tasmania and New South Wales as a fourth stock. However, the lateral line scale count variation could well reflect differences in the mean size of the fish analysed from different regions, rather than true stock differentiation.

Thus, when considering all the foregoing, there is some evidence that southern Tasmanian fish constitute one stock (*MPI** allele frequencies), Lord Howe Rise fish another stock (dorsal-fin ray counts), and there are insufficient data to determine whether fish from Western Australia, Great Australian Bight, and New South Wales constitute a single (third) stock or multiple stocks.

7.5. SPIKEY OREO, *NEOCYTTUS RHOMBOIDALIS*

Samples of spikey oreo were collected from eleven locations: Western Australia (one large and five small samples), Great Australian Bight (five small samples), South Australia (one sample), western Tasmania (one sample), southern Tasmania (two samples), eastern Tasmania (two large and one small sample), Bass Strait (one small sample), southern New South Wales (one small sample), northern New South Wales (one sample), Lord Howe Rise (one sample) and New Zealand (one sample) (Table 5.4). These samples were analysed for allozymes and mtDNA. Meristic counts were made on fish from all samples except those from the Great Australian Bight.

Liver degradation in the fish from the Great Australian Bight meant that the liver-specific allozymes were generally poorly resolved, and the quality of the DNA extracted from these fish was also poor. The combined Great Australian Bight sample and the small Bass Strait sample (n = 6) are not included in the main statistical analyses of the genetic data presented below. No significant allozyme or mtDNA differentiation was found between the multiple samples from either Western Australia or southern Tasmania, and so they were combined and treated in the analyses as single samples from each area; likewise, the two New South Wales samples were combined as one sample.

7.5.1. SPIKEY OREO: GENETIC DATA

Eight samples (WA, SA, WTAS, ETAS 1, ETAS 2, NSW, LHR, NZ) of spikey oreo were examined for the complete suite of allozyme characters (24 allozyme loci and a

general protein stain identifying 4 loci in addition to *CK-A**). Ten of the 28 loci showed no genetic variation within the individuals examined (Table 7.21.). Twelve loci were classed as polymorphic, with the frequency of the most common allele less than 0.950 in at least one sample. The other six loci (*sAAT-2*, *ESTD**, *sIDHP**, *LDH-C**, *LDH-1** and *PEP2**) showed very limited genetic variation. The average heterozygosity per locus was similar for each of the eight samples (Table 7.22).

Ten samples (WA, SA, WTAS, STAS, ETAS 1, ETAS 2, ETAS 3, NSW, LHR, NZ) were analysed for the twelve polymorphic loci (*mAAT**, *sAAT-1**, *CK-A**, *FH**, *GPI-A**, *GPI-B**, *G3PDH**, *MPI**, *PGDH**, *PGM-1**, *PGM-2** and *sSOD**). Only one significant deviation from Hardy-Weinberg equilibrium was observed, that was for *sSOD** in the South Australian sample (Table 7.23) which showed a heterozygote deficiency.

Significant differences in allele frequencies following chi-square heterogeneity tests among the ten samples were recorded at three loci, *PGM-1**, *MPI**, and *sSOD** (all $P<0.001$, see Table 7.24). The G_{ST} analyses, which compared the extent of genetic differentiation among samples, revealed significant results only at the *sSOD** locus ($P<0.001$), with the *PGM-1** and *MPI** loci being non-significant (probabilities of 0.055 and 0.082, respectively, Table 7.24).

Pairwise sample comparisons of the *PGM-1** data (Table 7.25) suggest that the observed heterogeneity arises primarily from the New Zealand sample, which has a slightly lower frequency of the *PGM-1*100* allele and a higher frequency of the *PGM-1*105* allele than any other sample. Comparing the New Zealand sample against all other samples combined yields a significant result ($\chi^2 = 21.995$ $P = 0.006$). Analysis of the remaining nine populations suggested further differentiation ($\chi^2 = 79.729$ $P = 0.007$). The Lord Howe Rise fish were not significantly different ($\chi^2 = 3.134$ $P = 0.750$) to the combined Australian sample, and removal of the Western Australian sample still left the remaining eight populations with significant differentiation ($\chi^2 = 66.175$ $P = 0.016$). The source of the differentiation at the *PGM-1** locus, apart from the separation of New Zealand, does not appear to be related to any other particular sample.

Similar pairwise sample comparisons of the *MPI** data (Table 7.25) suggest that Western Australia and New Zealand are genetically differentiated from the other samples, Western Australia with a higher frequency of *MPI*110* and New Zealand with a higher frequency of *MPI*100*. The Western Australia and South Australia samples were not significantly different to each other ($\chi^2 = 4.831$ $P = 0.191$) and so were grouped as one sample for further analysis. The six eastern Australia samples (WTAS, STAS, ETAS 1, ETAS 2, ETAS 3, and NSW) showed no evidence for differentiation ($\chi^2 = 12.807$ $P = 0.617$), nor was the Lord Howe Rise sample differentiated from the combined eastern Australia sample ($\chi^2 = 5.712$ $P = 0.170$). The combined eastern Australia plus Lord Howe Rise sample was significantly differentiated from both the combined western Australia sample (WA and SA; $\chi^2 = 24.968$ $P < 0.001$) and the New Zealand sample ($\chi^2 = 10.066$ $P = 0.029$). The *MPI** data therefore suggests three stocks of spikey oreo: western Australia (WA and SA), eastern Australia (WTAS, STAS, ETAS, NSW and LHR) and New Zealand.

The *sSOD** heterogeneity was far more striking than that of either *PGM-1** or *MPI**. This is particularly evident from the G_{ST} analyses (Table 7.24). About 43% of the allelic variation at the *sSOD** locus could be attributable to differentiation between samples, compared with less than 1% for *PGM-1** or *MPI**.

The pairwise comparisons for the *sSOD** locus (including the GAB sample, Table 7.26) revealed numerous significant differences between samples. The samples however fall into two major groups, as depicted in Figure 7.1, with one group having a frequency of the *sSOD*140* allele above 0.60 and the other group having a *sSOD*140* frequency of less than 0.25.

It can be seen from Figure 7.1. that there is no geographic basis for the two groups. For example, the high *sSOD*140* group includes samples from throughout the Australasian region, and although the low *sSOD*140* group primarily consists of Tasmanian samples, other Tasmanian samples are included in the high *sSOD*140* group. Furthermore, of three samples from East Tasmania, two are in the low group and one in the high group.

These same two groups are also strikingly apparent in a UPGMA-derived dendrogram of genetic distances at this locus (Fig. 7.2). The differences between samples within groups can be seen to be very much smaller than the differences between samples between the two groups.

Inspection of the catch records revealed that all samples with a high frequency of the **140* allele came from catches taken in a mean depth of more than 700 m (NSW, 850-1005 m; ETAS 3, 585-1185 m; WA, 600-900 m; NZ, 950 m; GAB, 850-1000 m; LHR, 740-800 m; STAS, 750-900 m) while the other group of samples were all from catches from a mean depth less than 700 m (SA, 700 m; ETAS 2, 500 m; ETAS 1, 440-550 m; WTAS, 540-630 m) (see Table 5.4*)*. Thus the *sSOD** differentiation relates not to horizontal spatial differentiation but to depth differentiation.

Figure 7.1. Spikey oreo. Diagrammatic representation of the significant differences observed between pairs of samples for the *sSOD** locus. Samples are positioned according to their *140 allele frequency, and the solid bars represent non-significant differences between samples connected by the bars.

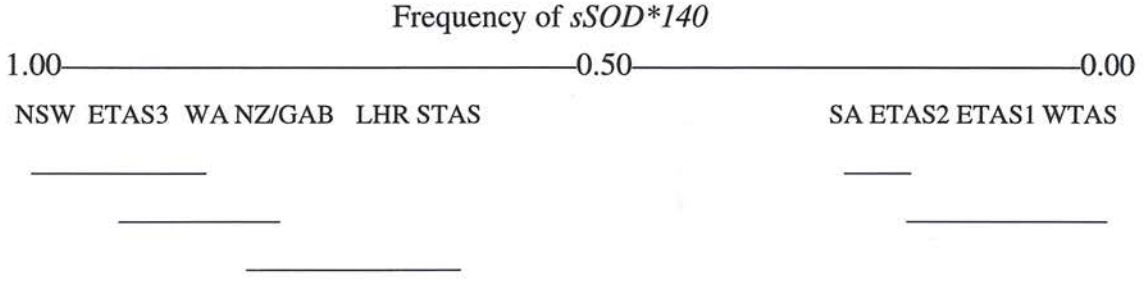
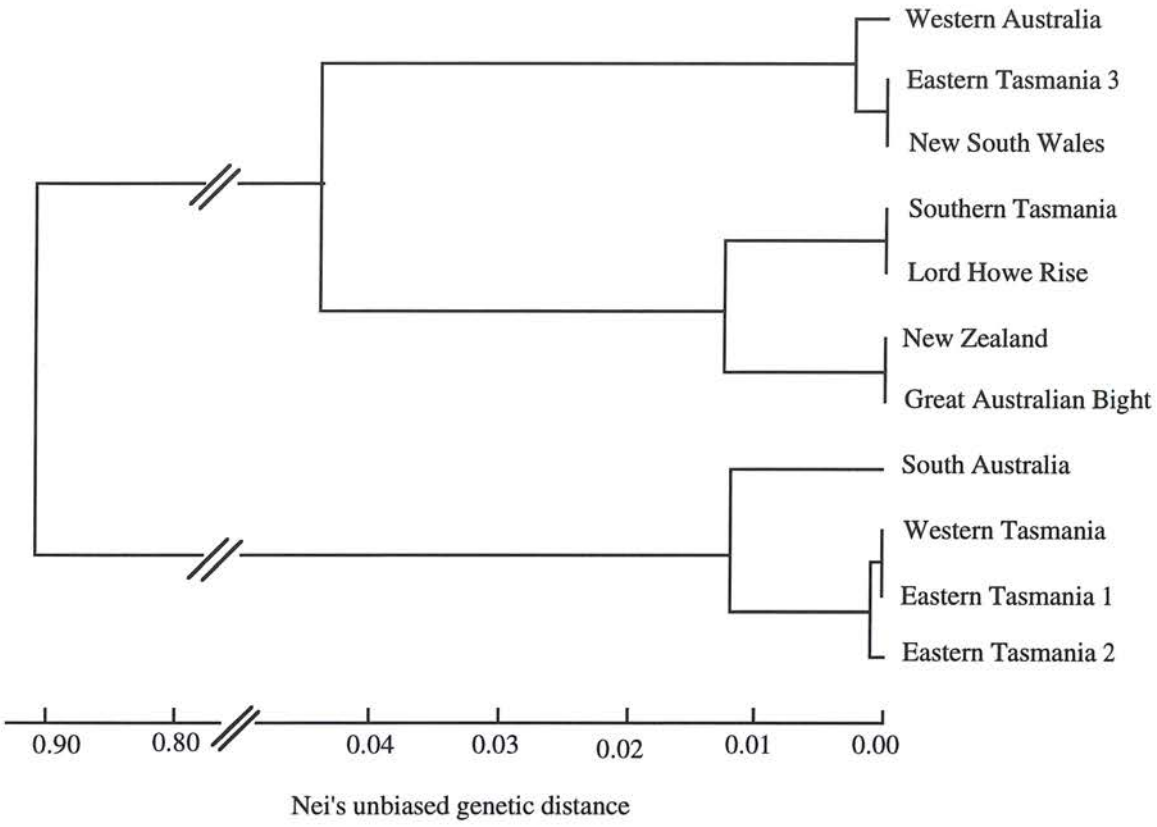


Figure 7.2. Spikey oreo. Dendrogram based on UPGMA clustering (unweighted pair-group method analysis) of Nei's (1978) unbiased genetic distance measure using allele frequencies at the *sSOD** locus alone.

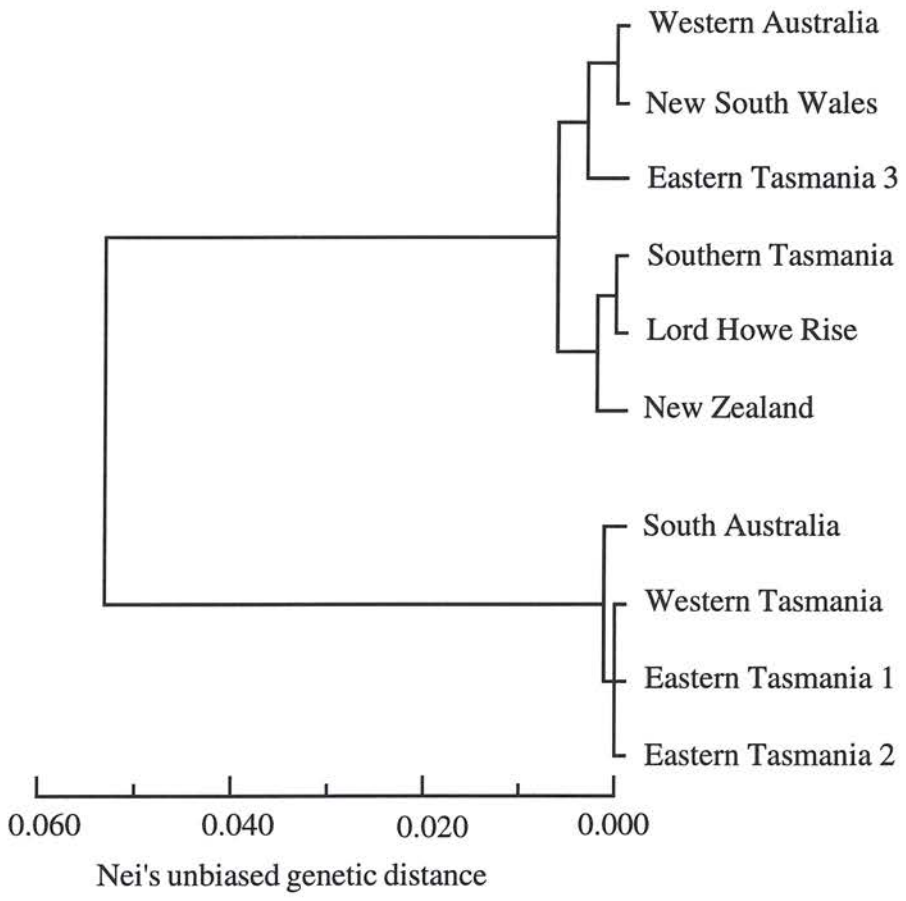


Interestingly, the one significant deviation from Hardy-Weinberg equilibrium that was recorded in spikey oreos was observed at the *sSOD** locus. This was the South Australian sample (Table 7.23) which showed a deficiency of heterozygotes. It is possible that this sample comprises individuals from the two groups identified at this locus. Such an admixture will create a heterozygote deficiency, as observed - the Wahlund effect. If there is an admixture, the proportions of the two groups making up the mixture can be estimated. Excluding the South Australian sample, the mean gene frequencies of the three shallow water samples (ETAS1, ETAS2, and WTAS) are *sSOD*140* 0.131, *sSOD*100* 0.869, and the mean gene frequencies of the eight deep water groups (WA, GAB, STAS, ETAS3, BS, NSW, LHR and NZ) are *sSOD*140* 0.800 and *sSOD*100* 0.200. A mix of 5 shallow: 1 deep will generate gene frequencies of *sSOD*140* 0.242 and sSOD**100* 0.758, very close to the observed South Australian gene frequencies of *sSOD*140* 0.243 and *sSOD*100* 0.757, and genotype proportions that accord very closely to those observed (Table 7.27). These fish were taken from 700 m on a submarine ridge south of Kangaroo Island (Table 5.4). Although locally referred to as "the Kangaroo Island Hill", it is more a ridge off the shelf than a true hill (Murray Cameron, pers. com.). It is significant here that this is not a regular area of continental slope, and is separated from the slope by deeper water. It is possible that

in this region both types of fish co-exist, or perhaps there were some depth differences between trawls. This putative mixture of types would account for the observed differentiation of this sample from the other three shallow water samples (Table 7.26).

Cluster analysis of the ten samples for the twelve polymorphic allozyme loci using Nei's (1978) unbiased genetic distance and UPGMA showed that the major separation of the samples is in line with the observed *sSOD** locus differences (Figure 7.3). The great bulk of the observed differentiation is in fact attributable to the *sSOD** differentiation.

Figure 7.3. Spikey oreo. Dendrogram based on UPGMA clustering (unweighted pair-group method analysis) of Nei's (1978) unbiased genetic distance measure using twelve polymorphic loci examined for ten samples. Samples from the upper group were caught in >700 m, from the lower group <700 m.



Two of the ten restriction enzymes (*Apa I, Ava I*) were used to examine mtDNA variation among the ten spikey oreo samples (Table 7.28). Fragment sizes were determined (Appendix 3). A total of 20 composite haplotypes was found. Two haplotypes each had an overall frequency of about 40%. Only one other haplotype was found in more than 10% of the individuals in any one sample. Eleven of the 20 haplotypes (55%) were detected only once. The haplotype diversity per sample ranged from 0.594 to 0.770, with a mean of 0.670, and nucleotide sequence diversity ranged from 0.009 to 0.018, with a mean of 0.012. No significant haplotype differentiation among samples was shown by either the chi-square (P = 0.406) or G_{ST} analysis (P = 0.557; Table 7.24).

There was no evidence from this mtDNA analysis (which was based on southern blotting of six-base restriction enzyme digests of the whole mtDNA molecule) for separation of the ten samples on a depth basis as described by the *sSOD** results. Pooling the four shallow samples (SA, ETAS1, ETAS2 and WTAS) and comparing this sample with the pooled deep sample (WA, STAS, ETAS3, NSW, LHR, NZ) also gave a non-significant result (χ^2 = 20.642, P =0.281). We decided to confirm or refute this lack of mtDNA differentiation by analysing mtDNA variation in a different manner, using PCR amplification and four-base restriction digests of the ND5/ND6 region of the molecule. Two 'deep' samples (ETAS 3 and LHR) and one 'shallow' sample (ETAS 2) were compared against one another (Table 7.29). Haplotype diversities per sample, although based on only two 4-base restriction enzymes, were similar to those shown by the two 6-base restriction enzyme analysis, ranging from 0.591 to 0.669, with a mean of 0.623. The important finding from this 4-base restriction enzyme analysis is that, like, the 6-base analysis, no significant differentiation among shallow and deep-water samples was detectable (χ^2 = 9.641 P = 0.479).

What are the conclusions to be drawn from these genetic analyses of stock structure in spikey oreos?

The allozyme analyses revealed both geographic (*PGM-1**, *MPI**) and depth heterogeneity (*sSOD**). The *PGM-1** and *MPI** results suggest that the New Zealand sample (taken off the east coast) is genetically differentiated from the Australian and Lord Howe Rise samples, and the *MPI** results further suggest some differentiation between western and eastern Australian samples. The *sSOD** results indicate that underlying this spatial heterogeneity is depth related differentiation; two discrete groups of spikey oreo exist, one with a high frequency of the *sSOD*140* allele occurring in deeper waters (>700 m), and another with a high frequency of the *sSOD*100* allele occurring in shallower waters (< 700 m). The ranges of these two groups overlap geographically (e.g. around Tasmania) and fish from the two groups appear to have been taken in a single fishing trip (i.e. South Australia sample).

Generally, such differentiation in allele frequencies between two groups of fish, even if only at a single locus, would be taken to indicate a severe restriction in gene flow between the groups. If this is the case for the *sSOD** heterogeneity described here, then the fact that the two groups overlap spatially (e.g. off the east coast of Tasmania and probably off South Australia), suggests reproductive isolation between the groups

and the possible existence of sibling species. However, if the two groups are reproductively isolated, perhaps for example they spawn at different depths, then differentiation of at least some other genetic markers would have been expected. In particular, the mtDNA genome would have been expected to show differences, as this is a fast evolving molecule (Brown *et al.*, 1979), and, for example, shows substantial differences among closely related tuna (*Thunnus*) species when allozyme differentiation is very limited (Elliott and Ward, 1995; Grewe, unpublished; Chow and Inoue, 1993; Ward *et al., 1995*). It is possible that the two groups have only very recently become reproductively isolated, say within the last 0.5 million years, and that insufficient time has passed to accumulate any detectable mtDNA differences or any allozyme differences other than at the *sSOD** locus.

The other possible explanation for these results is that natural selection is operating on the *sSOD** polymorphism. This hypothesis invokes a selective advantage for the *sSOD*140* allele (via its enzyme product) in deep water, and a selective advantage for the *sSOD*100* allele in shallower waters. Fish of the two groups spawn together, but either spend much of their life at the particular depth range 'preferred' by their *sSOD** allele, or distribution to depth is random but there is subsequent selective mortality of unfit genotypes. Under this latter scenario, selective mortality would have to be heavy, and selection of such intensity on allozyme polymorphisms is a very rare phenomenon. We are in fact unaware of any other similar examples.

Clearly these two hypotheses have different implications for management. The first hypothesis, reproductive isolation, posits two stocks, the second hypothesis, selective mortality, posits a single stock. The genetic data alone are compatible with either explanation. The more conservative management approach would be to assume the two stock hypothesis, and manage deep water spikey oreos separately from shallower water spikeys.

7.5.2. SPIKEY OREO: MERISTIC DATA.

Meristic counts were made on spikey oreo from twelve samples: Western Australia (WA), South Australia (SA), western Tasmania (WTAS), southern Tasmania (STAS), three samples from eastern Tasmania (ETAS 1, ETAS 2 and ETAS 3), Bass Strait (BS), two from New South Wales (NSW 1 and NSW 2), Lord Howe Rise (LHR), and New Zealand (NZ) (Table 7.30). The pyloric caeca were also counted from a further sample collected from the Great Australian Bight (GAB); these data are presented below.

Counts of pectoral-fin rays on the left and right side of the body did not differ significantly (n = 454, mean difference between left and right = -0.004, SD = 0.641, P = 0.884). Similarly, the total number of gill rakers did not differ between the left and right sides of the body (n = 456, mean difference (L-R) = 0.072, SD = 1.212; P = 0.203).

There were no significant differences between the ten samples (excluding BS and combining the two NSW samples) for the counts of dorsal-fin spines and rays (CD χ^2 = 148.221, P = 0.300) and anal fin spines and rays (CA χ^2 = 36.195, P = 0.416), nor for the total numbers of gill rakers on either side of the body (LTGR χ^2 = 93.255, P =

0.041; RTGR χ^2 = 71.127 P = 0.509). The result for the left side number of gill rakers was not significant after Bonferroni adjustment for multiple tests.

Lateral line counts on spikey oreo ranged from 89 to 121 (Table 7.30). The counts from the 12 samples were significantly differentiated ($P < 0.001$), with the NSW2 sample having a significantly higher count than most other samples.

NWS 2	vs	WA	$P = 0.002$
		SA	$P < 0.001$*
		WTAS	$P < 0.001$*
		STAS	$P < 0.001$*
		ETAS 1	$P = 0.007$
		ETAS 2	$P < 0.001$*
		ETAS 3	$P = 0.105$
		BS	$P = 0.238$
		NSW 1	$P = 0.078$
		LHR	$P = 0.008$
		NZ	$P = 0.016$

(* significant after Bonferroni adjustment for multiple tests).

The mean difference between other pairs of samples was not significant. Combining the two NSW samples reduces the mean count for that sample to 108.8 (SD±5.2), but this is still significantly higher than for the other samples.

Regressions and correlations of lateral line count against standard length were carried out (Table 7.31) for nine of the 12 samples (those where n>20). All were positive, although only two had P values of less than 0.05, and these became non-significant after applying Bonferroni corrections. However, the fact that all nine were positive is in itself a statistically significant result (χ^2 = 9, df=1, P = 0.003), indicating that there was a general tendency for larger fish to have higher lateral line scale counts. The NSW2 sample has the largest mean length of any of the nine samples tested for correlations, and it is likely that this was responsible for the higher counts of this sample rather than any true stock differentiation.

Spikey oreo had between 8 and 14 pyloric caeca (Table 7.30, GAB n = 39, mean = 10.80, SD = 1.28, range = 8–14). A significant difference was observed between the mean counts for each sample ($P < 0.001$). This differentiation was associated with the following pairs of samples, all of which were significantly different after adjustment for multiple tests ($P < 0.001$):

ETAS 1	>	LHR
ETAS 1	>	NSW 2
ETAS 1	>	ETAS 2
ETAS 1	>	ETAS 3
WTAS	>	ETAS 2
WTAS	>	ETAS 3.

Ten (those with n>20) of the 12 samples were tested for the presence of significant correlations and regressions of pyloric caeca counts on standard length (Table 7.31).

Eight of the correlations were positive, three with probabilities less than 5%. Bonferroni corrections for the ten multiple tests reduces the α level for significance to 0.005, and none is significant at this *P* value (although the largest sample, ETAS1, with *P*=0.006, borders on significance). Eight positive results and two negative results borders on significance (χ^2 = 3.6, df=1, *P* = 0.058). Thus there is arguably a slight tendency for larger fish to have higher pyloric caeca counts. However, this cannot account for the significant differences between pairs of samples listed above. For example, the ETAS1 fish had a smaller average size than those from LHR, ETAS2, ETAS3 and NSW2, and the WTAS fish also had a smaller average size than those from ETAS2 and ETAS3. This is therefore evidence for the ETAS2 sample coming from a different stock from the ETAS1/WTAS samples.

A special examination was made of the shallow and deep water samples which, as section 7.4.1. shows, were distinguishable by *sSOD** genotype.

Samples were pooled firstly into one of the two depth categories ('shallow' = WTAS, ETAS 1 and ETAS 2, 'deep' = WA, STAS, ETAS 3, NSW, LHR and NZ; the possibly mixed sample SA was not included in either group), and secondly into one of three *sSOD** genotypes (*sSOD*140/140*; *sSOD*140/100*; *sSOD*100/100*; the SA sample was included).

There was no differentiation observed for either depth grouping nor *sSOD** genotype for the combined dorsal-fin spine and ray counts, the combined anal-fin spine and ray counts, nor for the total gill raker counts on either side:

Depth grouping

combined dorsal fin counts	χ^2 = 10.841	*P* = 0.036
combined anal fin counts	χ^2 = 4.528	*P* = 0.332
total gill rakers (left)	χ^2 = 13.542	*P* = 0.093
total gill rakers (right)	χ^2 = 1.879	*P* = 0.988

*sSOD** genotype

combined dorsal fin counts	χ^2 = 10.303	*P* = 0.425
combined anal fin counts	χ^2 = 6.212	*P* = 0.416
total gill rakers (left)	χ^2 = 10.697	*P* = 0.377
total gill rakers (right)	χ^2 = 2.654	*P* = 0.988

However, significant differentiation was observed for both the lateral line and pyloric caeca counts. The 'deep' samples had a significantly (*P* = 0.006) higher mean lateral

line count than the 'shallow' samples (106.7 ± 5.2 compared to 105.3 ± 5.4), and this was reflected in the differentation observed between the *sSOD** genotypes. Here, the homozygotes for the **140* allele, present predominantly in the 'deep' samples, had a significantly ($P < 0.001$) higher mean lateral line count (107.3 ± 5.2) than either the heterozygotes (105.1 ± 5.9) or the **100* homozygotes (105.2 ± 4.9).

The 'shallow' samples had a significantly ($P < 0.001$) higher mean pyloric caeca count than the 'deep' samples (11.1 ± 1.2 compared to 10.8 ± 1.3), and again this was reflected in the *sSOD** analysis. The **100* allele homozygotes, predominant among the 'shallow' samples, had a significantly ($P < 0.001$) higher mean caeca count (11.2 ± 1.2) than the **140* homozygotes (10.7 ± 1.3). The heterozygotes (11.0 ± 1.1) were not differentated from either of the homozygotes.

The 'deep' sample fish were on average larger than the 'shallow' sample fish (ANOVA $P < 0.001$; 280.6 ± 61.7 mm compared to 268.4 ± 26.9 mm). Likewise, the **140* homozygote fish (284.0 ± 58.6 mm) were significantly ($P = 0.008$) larger than the **100* homozygote fish (274.6 ± 32.0 mm), but the heterozygote fish (278.3 ± 47.0 mm) were not significantly different from the two homozygous classes. As outlined earlier in this section, there appears to be a slight overall tendency for larger fish to have higher lateral line scale and pyloric caeca counts. This could account for the deep samples and the *sSOD*140* homozygote samples having a higher mean lateral line scale count than the shallow samples, but of course is in the wrong direction to account for the shallow samples and the *sSOD*100* homozygotes having a higher pyloric caeca count than the other samples. Thus the shallow and the *sSOD*100* homozygote samples do appear to show real differences in mean pyloric caeca count from the deepwater and *sSOD*140* samples, but the differences, although significant, are small in magnitude.

7.5.3. SPIKEY OREO: MORPHOMETRIC DATA.

Morphological measurements of the two homozygous *sSOD** genotypes were compared by analysis of variance for differences in body shape (see section 5.3). Sample sizes are given in Table 7.32. No significant interactions were found between stockgeno (see section 5.3) and ln(standard length). It was therefore accepted that the regression lines remained parallel for all stockgeno groups. The allometric growth equation was applied to all groups using the same ß value within each variable (Table 7.33).

Standardised values used in Anovas and Manovas produced only one significant interaction between stock and genotype (Table 7.34). This interaction, for the dependent variable ABL (anal fin base length), has been ignored because further investigation using Tukey's tests revealed that this interaction was significant in only ETAS1 and NSW, each of which had only one fish for one of the two genotypes. Therefore the interaction was based on an effective sample size of one. Further tests for the main effects of stock and genotype did not include an interaction term, and thus all stocks could be included in the analysis.

The effect of genotype was never significant (Table 7.34). This shows that the two *sSOD** homozygous genotypes (*sSOD*140/140* and *sSOD*100/100*) did not differ significantly in the morphometric traits examined.

Significant differences between stocks were found for 8 out of 13 variables (Table 7.34), but only two of these (HL and OD) remained significant after Bonferroni adjustment. A canonical variant analysis with sample as the grouping variable (and using fish of all three genotypes) revealed that, for example, the Lord Howe Rise and New South Wales samples appeared similar to one another and somewhat differentiated from the remaining samples (Figure 7.4). However, there was a lot of overlap between samples. A canonical variant analysis with depth as the grouping variable (deep: Western Australia, South Tasmania, East Tasmania 3, Bass Strait, New South Wales, Lord Howe Rise; shallow: West Tasmania, East Tasmania 1, East Tasmania 2; and keeping the possibly mixed South Australia sample as a separate group) showed some separation between the deep and shallow samples, but with appreciable overlap (Figure 7.5).

7.5.4. SPIKEY OREO: CONCLUSIONS

Interpreting the spikey oreo stock data is more difficult than for the other oreos. The fundamental question that has to be resolved is whether the depth-related *sSOD** genetic differences, which are very striking albeit restricted to a single locus, reflect reproductive isolation of two races of spikey oreos, or whether they reflect selection for different genotypes at different depths. We have conservatively, at least as regards sustainable management of the fishery, opted for the first explanation. The meristic and morphometric data show that these two 'races' also show small differences in pyloric caeca counts and perhaps also lateral line scale counts, and there are indications of body shape differences, but for all of these traits there are substantial overlaps between the 'races'. There were no differences for other meristic traits examined.

Within the deep water 'race', there is no good meristic evidence for any stock separation, but the Western Australia sample is distinguished by *MPI** allele frequencies, the New Zealand sample is distinguished both by *MPI** and *PGM-1** allele frequencies, while the other samples (South Tasmania, East Tasmania, New South Wales, Lord Howe Rise) cannot be distinguished from one another. This therefore argues for at least three deepwater stocks of spikey oreo: [Western Australia], [South Tasmania, East Tasmania 3, New South Wales, Lord Howe Rise], and [eastern coast of New Zealand].

Within the shallow water 'race' (including the South Australian sample which is predominantly of this type), there is no evidence of genetic stock separation (if the deepwater component of the South Australian sample is ignored). There is weak

meristic evidence (pyloric caeca) that the East Tasmania 2 sample is distinct from East Tasmania 1, West Tasmania, and South Australia. However, the close juxtaposition of the East Tasmania 1 and 2 samples argues against this conclusion, and it may be more likely that the shallow water race from South Australia to East Tasmania forms a single stock.

7.6. DISCUSSION

When samples of fish from different areas can be shown to differ genetically, this is strong evidence for stock structuring, brought about by a restriction in gene flow. Several instances of this in oreos have been described in the preceding sections. Repeat samplings are desirable to confirm such heterogeneity, but in the present project were not feasible due to time and financial constraints.

Meristic differentiation is generally seen as weaker evidence for stock heterogeneity. This is because the roles of genetic and environmental variation on the meristic variation cannot be distinguished (Lindsey, 1988). Thus spatial differences may be confounded by inter-yearly environmental differences and by different mixtures of year-classes among spatially distinct samples. Even if 0-group fish of a particular year are being compared (an impossibility at present for oreos), then the typically small differences in mean counts may reflect local differences in water temperature rather than true stock differentiation. For example, Hulme (1995), in reviewing past data on vertebral counts in North Sea herring (*Clupea harengus*), calculated the change in vertebral number at +0.11 per $1^{o}C$ rise in temperature, and concluded that vertebral counts alone should not be used as an independent character for identifying the origins of fish from different areas of the North Sea. Oreos live to an old age (probably >100 years, see Section 2), meaning that a particular sample is likely to contain a very wide spectrum of ages, and individuals cannot be accurately assigned to a specific year class. Furthermore, most of the significant meristic differences we observed in oreos arose from variation in pyloric caeca and lateral line scale counts, but few from fin spine and ray count differences: the former characteristics may well be laid down later in life (Lindsey, 1988) and therefore subjected to greater environmental influences than the latter. Environmental effects on body shape are likely to be still more marked. We are therefore inclined to put less weight on the small differences in meristic and morphometric traits that we observed than on the observations of genetic differentiation.

One problem with our datasets is that not all samples could be analysed for all traits. Some samples arriving at Hobart had been poorly treated, generally meaning that in such samples not all genetic traits could be reliably examined. In particular, liver-specific allozymes had sometimes degraded. On occasion, reliable meristic counts could not be taken. This meant that a full, orthogonal, comparison of all traits in all samples was not possible. Another problem is that sometimes sample sizes were less than ideal.

Any estimates of stock numbers based on genetic data should be regarded as minimal estimates. While genetic differences between samples indicate multiple stocks, the failure to find differences does not necessarily indicate a single stock. Genetic differentiation is powerful evidence of stock structure; the lack of differentiation is consistent with but does not prove a single stock. Carvalho and Hauser (1994) enumerate five causes for a lack of genetically detectable stock separation:

(i) Sufficient gene flow to maintain panmixia. Note that even quite low rates of genetic exchange are sufficient to reduce heterogeneity to levels that would not be statistically detectable with sample sizes in the normal region of 100 individuals. Rates of exchange of 5-10% would be extremely hard to detect genetically, but from a management point of view such populations may be best managed as independent stocks.

(ii) Sporadic recruitment from distant areas which could produce the appearance of panmixia but the areas may be best managed as independent stocks.

(iii) Similar environmental conditions giving rise to stabilising selection and similar gene frequencies in reproductively isolated stocks. Managing such stocks as a single unit stock would be wrong.

(iv) Recent divergence of populations giving insufficient time for detectable differentiation to have occurred. Again, treating such stocks as a single unit stock would be wrong.

(v) Failure to detect true genetic differentiation because of the techniques employed or inadequate sample sizes. Again, treating such stocks as a single unit stock would be wrong.

It is operationally very hard to distinguish among these hypotheses. Therefore, in cases when genetic differentiation cannot be detected, it is especially important to consider data from non-genetic sources. In the oreos, there is very little useful stock structure information other than that described in this Report.

So, given these caveats, what conclusions concerning stock structures in oreos could be drawn?

Black oroes: there is evidence that the New Zealand sample constitutes a stock distinct from the Australian (southern Tasmania, Western Australia) stock. This conclusion is based on a (just) significant difference in mtDNA haplotype frequencies (with no detected allozyme differences), supported by differences in pyloric caeca and lateral line scale counts.

Smooth oreos: there was no genetic evidence of stock structuring, with only lateral line scale counts distinguishing a Western Australia sample from southern Tasmanian, Lord Howe Rise, and New Zealand samples. This should be seen as only suggestive of

stock heterogeneity.

Warty oreos: no New Zealand sample was forthcoming, but allele frequencies at the allozyme locus *MPI** differentiated a southern Tasmanian sample from samples from Western Australia and New South Wales. Whether there are multiple stocks within Western Australia, Great Australian Bight and New South Wales is not yet clear. Differences in dorsal-fin spine and ray counts and lateral line scales suggest that the Lord Howe Rise sample might be from a stock distinct from the fore-going.

Spikey oreos: two depth-separated races were detected, primarily distinguishable by striking differences in *sSOD** allele frequencies. Three stocks of the deep-water race were identified: Western Australia (distinguished by *MPI**), New Zealand (distinguished by *MPI** and *PGM-1**), and southern Tasmania, East Tasmania 1, New South Wales and Lord Howe Rise. There was no evidence for the shallow-water samples (East Tasmania 2 and 3, West Tasmania, and South Australia) constituting more than a single stock.

Before discussing these results, it is worth pointing out that in the oreos, the mtDNA analyses were, if anything, somewhat less useful in delineating stocks than the allozyme analyses. When mtDNA analyses were first used for analysing population structures, early results were very encouraging and appeared to provide greater resolution than allozyme analysis (see Ward and Grewe, 1994). This was attributed to the smaller effective population size of mtDNA (being haploid and maternally inherited) and its rapid rate of evolution. However, more recently it has been shown that mtDNA analysis does not always lead to enhanced resolution of stock issues (see Ward and Grewe, 1994), and this appears to hold true for the oreos. In cases where genetic differentiation is expected to be low, the ability of allozyme analysis to provide a reasonable number of independent loci is an important advantage over mtDNA analysis which is effectively, a single marker.

The extent of genetic inter-sample differentiation within the oreo species, with the exception of the *sSOD** deep-shallow water separation of spikey oreos, was always very low. This was true for both allozyme and mtDNA analyses. While some distinct stocks could be identified, generally less than 1% (after correction for sample size) of the allozyme or mtDNA variation could be attributed to among-sample differentiation. This is perhaps not unexpected of marine fish species with long life spans and pelagic juveniles. Oreos are in these respects similar to orange roughy, *Hoplostethus atlanticus*, and in this species too the extent of genetic differentiation between areas is very limited (Elliott and Ward, 1992; Elliott *et al.*, 1994)[1].

A number of other commercial fisheries have been investigated for evidence of genetically based stock structuring in southern Australia. Generally, these, like the oreos, show little evidence for restricted gene flow in this area. Studies of orange

[1] Although there is evidence that roughy from the south and south-east of New Zealand are genetically distinct from roughy from more northern areas of New Zealand and from Tasmania (Smith, McVeagh and Ede, unpublished).

roughy, *Hoplostethus atlanticus*, found allozyme homogeneity in samples from Western Australia to New South Wales (Elliott and Ward, 1992). Mitochondrial DNA studies revealed similar homogeneity using restriction enzymes that cut DNA at six-base sequences, but separated a New South Wales stock from all others using four-base cutters (Smolenski *et al.*, 1993). Samples of jackass morwong, *Nemadactylus macropterus*, from Western Australia to New South Wales, were genetically homogeneous using both allozyme and mtDNA analyses (Elliott and Ward, 1994; Grewe *et al.*, 1994). Allozyme studies of blue eye trevalla, *Hyperoglyphe antarctica*, from South Austalia to New South Wales similarly failed to reveal evidence of stock heterogeneity, although this study did identify a second and previously unrecognised species in the New South Wales component of the fishery (Bolch *et al.*, 1993). In complete distinction to these results was the genetic analysis of the gemfish, *Rexea solandri* (Paxton and Colgan, 1993) Two distinct stocks were detected, a southern/western stock and an eastern stock. These stocks were distiguishable by alternative common alleles at an allozyme locus (*AAT-2**), but far more strikingly, all eleven restriction enzymes tested gave highly significant differences in mtDNA fragment profiles.

Looking further afield, there have been several comparative studies of Australian and New Zealand fisheries separated by the Tasman Sea. This has been shown to be a partial barrier to gene flow in several marine fish and shellfish (e.g. blue grenadier, *Macruronus novaezelandiae* using allozymes [Milton and Shaklee, 1987] but not mtDNA [Smith, McVeagh and Ede, unpublished], jackass morwong, *Nemadactylus macropterus* using allozymes [Elliott and Ward, 1994] and mtDNA [Grewe *et al.*, 1994], snapper, *Chrysophrys auratus,* using allozymes [MacDonald, 1980], rock lobster, *Jasus verreauxi* using mtDNA [Brasher *et al.*, 1992], *Jasus edwardsii* using allozymes [Smith *et al., 1*980] but not mtDNA [Ovenden *et al., 1*992]). There are, however, exceptions (e.g. orange roughy using allozymes [Elliott and Ward, 1992] and mtDNA [Smith, McVeagh and Ede, unpublished], gemfish using allozymes and mtDNA [Paxton and Colgan, 1993]). In the gemfish study, New Zealand fish were found to be similar to eastern Australian fish, although few New Zealand fish were analysed.

With respect to the oreos, three species were examined from both sides of the Tasman, with the New Zealand samples coming from the east of the South Island (Chatham Rise). Two of these showed evidence of differentiation: black oreos (just significant mtDNA differences but no allozyme differences) and (deep water) spikey oreos (allozyme differences - *MPI** and *PGM-1** - but no mtDNA differences). In both species the degree of differentiation was low, and it is unsurprising that only a small minority of genetic traits showed detectable differences. Such results emphasise the need for tests of multiple loci (while making appropriate corrections for using multiple tests), and justify our strategy of analysing both allozyme and mtDNA variation. The third tested species, the smooth oreo, despite good samples from both Australia and New Zealand, showed no significant differentiation.

Figure 7.4. Spikey oreo. Canonical variate analyses of the pooled sample and individual samples.

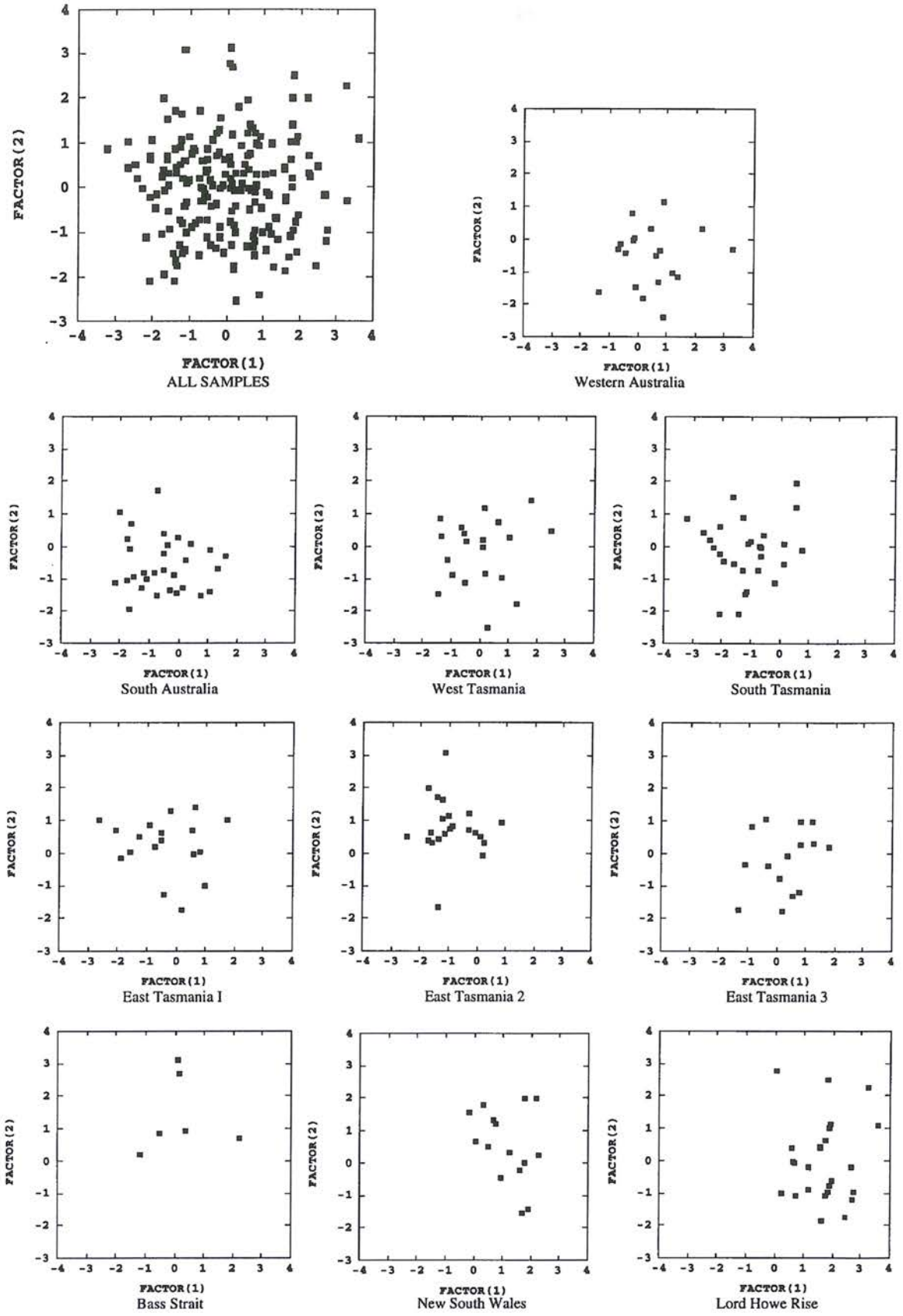


Figure 7.5. Spikey oreo. Canonical variate analyses of the pooled sample and three depth samples.

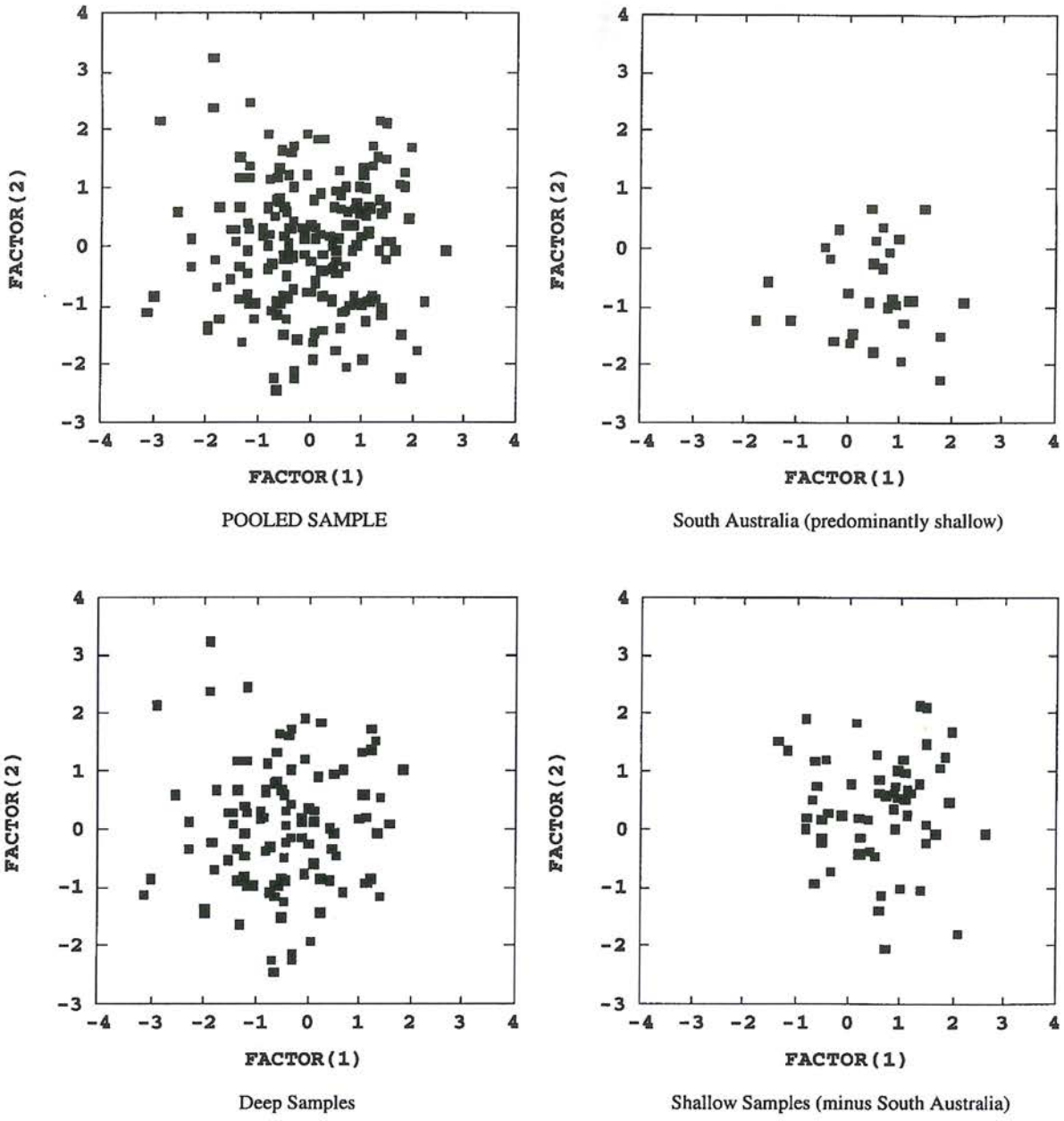


Table 7.1. Black oreos. Allele frequencies and numbers of fish. n.a.=not analysed

Locus	Allele	STAS	NZ	S.TAS.R.
Variable loci				
*CK-A**	*100*	0.866	0.898	0.845
	90	0.134	0.102	0.155
	n	*202*	*93*	*42*
*FH**	*120*	0.005	-	
	100	0.990	0.989	
	80	0.005	0.011	
	n	*201*	*93*	*n.a.*
*G3PDH-2**	*130*	0.128	0.097	
	100	0.555	0.574	
	75	0.317	0.330	
	n	*191*	*88*	*n.a.*
*LDH-2**	*100*	0.062	0.038	0.037
	50	0.938	0.962	0.963
	n	*202*	*93*	*41*
*PGDH**	*110*	0.642	0.650	
	100	0.294	0.267	
	75	0.063	0.083	
	n	*197*	*90*	*n.a.*
*PGM-1**	*100*	0.015	-	
	95	0.715	0.648	
	90	0.249	0.333	
	85	0.021	0.019	
	n	*195*	*81*	*n.a.*
*PGM-2**	*120*	0.005	0.011	-
	100	0.598	0.583	0.573
	80	0.279	0.289	0.280
	65	0.103	0.117	0.134
	50	0.015	-	0.012
	n	*199*	*90*	*41*
*sSOD**	*140*	0.187	0.206	0.280
	100	0.813	0.794	0.720
	n	*198*	*90*	*41*
Invariant loci: alleles and sample sizes				
*mAAT**	*-100*	*202*	*24*	*n.a.*
*sAAT-2**	*100*	*202*	*24*	*n.a.*
*ADH**	*100*	*202*	*24*	*n.a.*
*AK**	*100*	*202*	*24*	*n.a.*
*ESTD**	*115*	*202*	*24*	*n.a.*
*GPI-B**	*100*	*202*	*24*	*n.a.*
*mIDHP**	*100*	*202*	*24*	*n.a.*
*sIDHP**	*100*	*202*	*24*	*n.a.*
*LDH-1**	*100*	*202*	*24*	*n.a.*
*LDH-C**	*100*	*202*	*24*	*n.a.*
*sMDH-1**	*100*	*202*	*24*	*n.a.*
*sMDH-2**	*100*	*202*	*24*	*n.a.*

Table 7.1. continued

*sMEP**	*x*	*202*	*24*	*n.a.*
*MPI**	*90*	*202*	*24*	*n.a.*
*PEP1-1**	*100*	*202*	*24*	*n.a.*
*PEP2**	*100*	*202*	*24*	*n.a.*
*PROT-1**	*x*	*202*	*24*	*n.a.*
*PROT-2**	*x*	*202*	*24*	*n.a.*
*PROT-4**	*x*	*202*	*24*	*n.a.*

Table 7.2. Black oreo. Summary allozyme statistics for the two samples in which all 27 loci were scored. Mean and standard deviation provided. Mean heterozygosity is Nei's (1978) unbiased estimate. % poly = the percentage of loci polymorphic, where the frequency of the most common allele is less than 0.95.

Sample	Sample size	No. alleles	% poly	Heterozygosity
southern Tasmania	200.9 ± 0.5	1.6 ± 0.2	25.9	0.101 ± 0.037
New Zealand	43.5 ± 5.9	1.5 ± 0.2	22.2	0.100 ± 0.037

Table 7.3. Black oreo. Composite mitochondrial DNA haplotypes, frequencies, sample sizes (n), haplotype (nucleon) diversities (h) and nucleotide diversities (n.d.). Restriction enzyme order *Ava* I, *Bst* EII, *Dra* I, *Eco* RI, *Hind* III, *Kpn* I, *Pst* I, *Pvu* II, *Sty* I and *Xba* I.

mtDNA haplotype	STAS	NZ
ADAEBAAAAA	0.094	0.145
ADAEBCAAAA	0.781	0.711
ADAEBCABAA	0.063	-
ADAEFCAAAA	0.042	0.066
AFAEBCAAAA	0.010	-
CDBEBCAAAA	0.010	-
ADAEBCAABA	-	0.013
ADAECCAAAA	-	0.013
ADDEBCAAAA	-	0.026
AFAABCAAAA	-	0.013
CDDEBCAAAA	-	0.013
n	*96*	*76*
h	0.379	0.474
n.d.	0.0012	0.0015

Table 7.4. Black oreo. Analyses of genetic differentiation. H_S = average Hardy-Weinberg expected heterozygosity (genetic diversity for mtDNA) per sample. G_{ST} = proportion of genetic variation attributable to inter-sample differentiation.

	Number of			Chi-square analysis		Genetic diversity analysis		
Loci	**alleles**	**fish**	H_S	$\chi 2$	P	G_{ST}	$G_{ST.null} \pm SD$	P
(a) Tasmania and New Zealand								
*CK-A**	2	295	0.208	1.167	0.292	0.002	0.002 ± 0.003	0.251
*FH**	3	294	0.021	1.546	0.515	<0.001	0.002 ± 0.002	0.707
*G3PDH-2**	3	279	0.564	1.161	0.567	<0.001	0.002 ± 0.002	0.711
*LDH-2**	2	295	0.094	1.460	0.264	0.003	0.002 ± 0.003	0.192
*PGDH**	3	287	0.498	1.046	0.595	<0.001	0.002 ± 0.002	0.679
*PGM-1**	4	276	0.447	6.255	0.083	0.007	0.002 ± 0.003	0.084
*PGM-2**	5	289	0.558	3.681	0.481	<0.001	0.002 ± 0.002	0.870
*sSOD**	2	288	0.315	0.278	0.665	<0.001	0.002 ± 0.003	0.608
mtDNA	13	172	0.427	15.615	0.034	0.008	0.006 ± 0.005	0.223
(b) Tasmania, South Tasman Rise, and New Zealand								
*CK-A**	2	337	0.226	1.772	0.396	0.004	0.004 ± 0.004	0.361
*LDH-2**	2	336	0.086	1.971	0.395	0.003	0.005 ± 0.005	0.505
*PGM-2**	5	330	0.564	4.821	0.752	<0.001	0.005 ± 0.004	0.981
*sSOD**	2	329	0.345	3.677	0.170	0.009	0.005 ± 0.005	0.126

Table 7.5. Black oreo. Meristic data from three samples. See text for character abbreviations and Table 5.1 for sample details. (min = minimum count, max = maximum count, SD = standard deviation around mean, n = number of individuals for which character was scored)

Sample		DS	DR	DC	AS	AR	AC	LVS	LVR	RVS	RVR	LP	RP	LUGR	LMGR	RLGR	LTGR	RUGR	RMGR	RLGR	RTGR	LL	PC
WA	mean	6.11	31.80	38.00	2.80	30.10	32.90	1.00	6.00	1.00	6.00	19.00	19.22	6.78	1.00	25.25	31.70	6.56	1.00	24.56	31.20	96.80	11.71
	min	5	31	37	2	28	31	1	6	1	6	17	17	5	1	24	29	5	1	23	29	90	10
	max	7	33	39	3	32	35	1	6	1	6	20	21	10	1	27	35	8	1	26	33	107	14
	SD	0.60	0.79	0.87	0.42	0.99	1.10	0.00	0.00	0.00	0.00	1.00	1.20	1.64	–	1.17	2.16	1.24	–	1.01	1.40	5.77	1.38
	n	9	10	9	10	10	10	10	10	10	10	9	9	9	1	8	10	9	1	9	10	10	7
STAS	mean	6.80	32.02	38.82	2.95	29.65	32.60	1.00	5.98	1.00	6.00	19.15	19.06	6.15	1.00	24.23	31.13	6.22	1.00	23.96	30.91	102.31	11.63
	min	6	30	37	2	28	31	1	5	1	6	18	17	5	1	21	28	5	1	21	28	93	9
	max	8	34	41	3	31	34	1	6	1	6	21	21	7	1	29	36	8	1	27	35	116	16
	SD	0.53	0.81	0.78	0.23	0.73	0.76	0.00	0.14	0.00	0.00	0.77	0.79	0.60	0.00	1.58	1.53	0.63	0.00	1.55	1.66	4.90	1.40
	n	54	54	54	55	55	55	55	55	55	55	53	54	53	40	53	53	54	39	54	54	55	198
NZ	mean	6.44	32.00	38.44	3.00	29.22	32.22	1.00	5.89	1.00	6.00	18.56	18.44	6.33	1.00	22.89	29.78	6.67	1.00	22.67	29.56	97.78	13.33
	min	6	30	37	3	28	31	1	5	1	6	18	18	6	1	22	28	6	1	21	28	88	12
	max	7	34	40	3	30	33	1	6	1	6	19	19	8	1	25	33	8	1	24	32	106	15
	SD	0.53	1.12	0.88	0.00	0.67	0.67	0.00	0.33	0.00	0.00	0.53	0.53	0.71	0.00	1.17	1.86	0.71	0.00	1.23	1.33	5.33	0.87
	n	9	9	9	9	9	9	9	9	9	9	9	9	9	5	9	9	9	2	9	9	9	9

Table 7.6. Black oreo. Correlations of pyloric cecae and lateral line scale counts with length. Note, data only shown for samples with n>20.

sample	n	mean length	mean count	regression analysis			
				intercept	slope	correlation coefficient	*P*
Pyloric cecae							
STAS	203	31.751	11.596	10.310	0.040	0.090	0.201
Lateral line scales							
STAS	45	31.487	102.644	92.825	0.312	0.235	0.121

Table 7.7. Smooth oreo. Allele frequencies and numbers of fish.

Locus	Allele	WA	STAS	NZ
Variable loci				
*mAAT**	*-100*	0.959	0.954	0.969
	-200	0.041	0.046	0.031
	n	*97*	*218*	*98*
*sAAT-1**	*100*	0.974	0.962	0.949
	80	0.026	0.038	0.051
	n	*97*	*199*	*99*
*sAAT-2**	*100*	0.979	0.988	1.000
	80	0.021	0.008	-
	60	-	0.005	-
	n	*24*	*200*	*24*
*FH**	*115*	0.005	0.007	0.010
	110	0.036	0.023	0.025
	100	0.832	0.838	0.843
	80	0.128	0.132	0.121
	n	*98*	*216*	*99*
*LDH-C**	*100*	0.799	0.807	0.791
	85	0.201	0.193	0.209
	n	*97*	*218*	*98*
*LDH-1**	*100*	0.763	0.771	0.800
	40	0.237	0.229	0.200
	n	*97*	*218*	*100*
*MPI**	*100*	0.117	0.146	0.076
	90	0.883	0.854	0.924
	n	*90*	*206*	*92*
*PEP1-1**	*90*	1.000	0.998	1.000
	80	-	0.003	-
	n	*24*	*200*	*24*

Table 7.7. continued. Smooth oreo. Allele frequencies and numbers of fish

Locus	Allele	WA	STAS	NZ
*PEP2**	*100*	0.516	0.507	0.500
	85	0.484	0.493	0.500
	n	*96*	*217*	*89*
*PGDH**	*100*	0.918	0.940	0.938
	90	0.031	0.032	0.036
	85	0.051	0.028	0.026
	n	*98*	*217*	*97*
*PGM-1**	*95*	0.011	0.019	0.016
	90	0.582	0.636	0.632
	85	0.049	0.021	0.011
	80	0.357	0.324	0.341
	n	*91*	*213*	*91*
*PGM-2**	*120*	-	0.002	0.005
	100	0.896	0.867	0.870
	80	0.104	0.131	0.125
	n	*96*	*218*	*100*
*sSOD**	*180*	0.368	0.385	0.354
	140	0.632	0.615	0.646
	n	*95*	*218*	*99*
Invariant loci: alleles and sample sizes				
*ADH**	*125*	*24*	*200*	*24*
*AK**	*100*	*24*	*200*	*24*
*CK-A**	*90*	*24*	*200*	*24*
*ESTD**	*115*	*24*	*200*	*24*
*GPI-B**	*100*	*24*	*200*	*24*
*G3PDH-2**	*70*	*24*	*200*	*24*
*mIDHP**	*100*	*24*	*200*	*24*
*sIDHP**	*100*	*24*	*200*	*24*
*LDH-2**	*100*	*24*	*200*	*24*
*sMDH-1**	*100*	*24*	*200*	*24*
*sMDH-2**	*100*	*24*	*200*	*24*
*sMEP**	*x*	*24*	*200*	*24*
*PROT-1**	*x*	*24*	*200*	*24*
*PROT-2**	*x*	*24*	*200*	*24*
*PROT-3**	*x*	*24*	*200*	*24*
*PROT-4**	*x*	*24*	*200*	*24*

Table 7.8. Smooth oreo. Summary allozyme statistics for the three samples in which all 29 loci were scored. Mean and standard deviation provided. Mean heterozygosity is Nei's (1978) unbiased estimate. % poly = the percentage of loci polymorphic, where the frequency of the most common allele is less than 0.95.

Sample	Sample size	No. alleles	% poly	Heterozygosity
Western Australia	51.2 ± 6.6	1.6 ± 0.2	31.0	0.110 ± 0.032
southern Tasmania	205.4 ± 1.5	1.7 ± 0.2	31.0	0.110 ± 0.032
New Zealand	51.5 ± 6.7	1.6 ± 0.2	34.5	0.101 ± 0.030

Table 7.9. Smooth oreo. Composite mitochondrial DNA haplotypes, frequencies, sample sizes (n), haplotype (nucleon) diversities (h) and nucleotide diversities (n.d.). Restriction enyme order *Eco* RI and *Hind* III.

mtDNA haplotype	WA	STAS	NZ	LHR
CD	0.517	0.621	0.528	0.667
CE	0.319	0.242	0.352	0.133
DD	0.165	0.137	0.121	0.200
n	*91*	*95*	*91*	*15*
h	0.614	0.541	0.593	0.533
n.d.	0.0105	0.0087	0.0097	0.0088

Table 7.10. Smooth oreo. Analyses of genetic differentiation. H_S = average Hardy-Weinberg expected heterozygosity (genetic diversity for mtDNA) per sample. G_{ST} = proportion of genetic variation attributable to inter-sample differentiation.

	Number of			Chi-square analysis		Genetic diversity analysis		
Loci	**alleles**	**fish**	H_S	$\chi 2$	P	G_{ST}	$G_{ST.null} \pm SD$	P
(a) Western Australia, southern Tasmania and New Zealand samples								
*mAAT**	2	413	0.075	0.778	0.648	0.001	0.003 ± 0.003	0.670
*sAAT-1**	2	395	0.073	1.642	0.401	0.003	0.003 ± 0.003	0.401
*sAAT-2**	3	248	0.022	1.864	0.833	0.007	0.008 ± 0.005	0.592
*FH**	4	413	0.281	1.309	0.970	<0.001	0.003 ± 0.002	0.974
*LDH-C**	2	413	0.321	0.242	0.892	<0.001	0.003 ± 0.003	0.900
*LDH-1**	2	415	0.345	0.926	0.603	0.002	0.003 ± 0.003	0.564
*MPI**	2	388	0.199	5.798	0.048	0.008	0.003 ± 0.003	0.057
*PEP1-1**	2	248	0.002	0.240	1.000	0.002	0.004 ± 0.005	0.649
*PEP2**	2	402	0.500	0.091	0.954	<0.001	0.003 ± 0.003	0.940
*PGDH**	3	412	0.129	2.798	0.622	0.002	0.003 ± 0.002	0.571
*PGM-1**	4	395	0.502	7.489	0.285	0.002	0.003 ± 0.003	0.533
*PGM-2**	3	414	0.215	1.923	0.810	0.001	0.003 ± 0.003	0.608
*sSOD**	2	248	0.465	0.618	0.723	<0.001	0.003 ± 0.003	0.764
mtDNA	3	277	0.575	3.698	0.450	0.008	0.008 ± 0.006	0.368
(b) Western Australia, southern Tasmania, New Zealand and Lord Howe Rise								
mtDNA	3	292	0.556	5.783	0.442	0.021	0.018 ± 0.013	0.301

Table 7.11. Smooth oreo. Meristic data from four samples. See text for character abbreviations and Table 5.2 for sample details. (min = minimum count, max = maximum count, SD = standard deviation around mean, n = number of individuals for which character was scored)

Sample		DS	DR	DC	AS	AR	AC	LVS	LVR	RVS	RVR	LP	RP	LUGR	LMGR	LLGR	LTGR	RUGR	RMGR	RLGR	RTGR	LL	PC
WA	mean	5.59	34.20	39.79	2.72	31.93	34.61	1.00	4.98	1.00	4.95	20.60	20.66	6.12	1.00	19.16	25.74	6.07	1.00	18.93	25.47	117.14	178.92
	min	5	32	37	2	28	31	1	4	1	4	19	19	5	1	17	23	5	1	17	23	100	97
	max	7	36	41	3	34	37	1	5	1	5	22	23	8	1	22	29	7	1	22	29	133	262
	SD	0.53	1.00	0.87	0.45	1.07	0.98	0.00	0.13	0.00	0.22	0.67	0.72	0.68	0.00	0.86	1.32	0.62	0.00	0.94	1.28	7.86	38.83
	n	56	56	56	57	58	57	58	58	58	58	58	58	57	26	57	57	57	27	57	57	51	38
STAS	mean	5.36	34.04	39.41	2.55	32.06	34.60	1.00	4.98	1.00	4.98	20.76	20.53	6.67	1.00	19.04	25.72	6.58	–	19.25	25.84	108.15	170.03
	min	5	29	35	2	30	32	1	4	1	4	19	18	5	1	17	23	5	–	17	22	98	75
	max	6	36	41	3	34	37	1	5	1	5	22	22	8	1	22	29	8	–	22	30	129	299
	SD	0.48	1.19	1.08	0.50	1.00	0.93	0.00	0.14	0.00	0.14	0.82	0.84	0.70	–	0.97	1.37	0.83	–	1.19	1.60	6.36	42.29
	n	53	52	51	55	52	52	51	50	50	50	54	55	55	1	54	54	55	0	55	55	40	184
LHR	mean	5.60	33.60	39.20	3.00	31.54	34.54	1.00	5.00	1.00	5.00	20.13	20.53	6.80	1.00	19.67	26.60	6.87	–	19.00	25.87	107.86	191.36
	min	5	32	38	3	31	34	1	5	1	5	15	19	5	1	18	24	6	–	17	23	100	132
	max	6	35	41	3	33	36	1	5	1	5	22	22	9	1	22	31	8	–	22	30	117	269
	SD	0.51	0.83	0.94	0.00	0.78	0.78	0.00	0.00	0.00	0.00	1.64	0.74	1.21	0.00	1.11	1.88	0.64	–	1.46	1.73	5.42	34.88
	n	15	15	15	15	13	13	15	15	15	15	15	15	15	2	15	15	15	0	15	15	14	14
NZ	mean	5.67	34.56	40.22	2.11	32.56	34.67	1.00	5.00	1.00	5.00	20.33	20.44	5.56	1.00	18.44	24.56	5.44	1.00	19.22	25.11	–	167.56
	min	5	33	39	2	31	33	1	5	1	5	19	19	5	1	17	23	5	1	17	22	–	126
	max	7	35	41	3	34	36	1	5	1	5	21	21	6	1	20	27	6	1	22	28	–	225
	SD	0.71	0.73	0.67	0.33	1.13	1.00	0.00	0.00	0.00	0.00	0.71	0.73	0.53	0.00	1.13	1.51	0.53	0.00	1.72	2.15	–	37.79
	n	9	9	9	9	9	9	9	8	9	9	9	9	9	5	9	9	9	4	9	9	0	9

Table 7.12. Smooth oreo. Correlations of pyloric cecae and lateral line scale counts with length. Note, correlations only given for samples with n>20.

sample	n	mean length	mean count	regression analysis			
				intercept	slope	correlation coefficient	*P*
Pyloric cecae							
LHR	23	46.626	191.957	69.879	2.618	0.445	0.033
STAS	198	32.288	171.258	150.541	0.642	0.071	0.318
STAS Rise	53	24.685	185.264	118.756	2.694	0.403	0.003
WA	39	42.079	180.462	126.381	1.285	0.129	0.435
Lateral line scales							
STAS	40	33.065	108.150	114.960	-0.206	-0.153	0.345
WA	51	42.239	117.137	122.231	-0.121	-0.069	0.632

Table 7.13. Warty oreo. Allele frequencies and numbers of fish. n.a.=not analysed

Locus	allele	WA IV	STAS	NSW	SAFR	WA I	WA II	WA III	WA V	GAB	LHR
Variable loci											
*sAAT-2**	*100*	1.000	0.991	1.000	1.000						
	80	-	0.005	-	-						
	60	-	0.005	-	-						
	n	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*CK-A**	*110*	0.843	0.861	0.906	0.909	0.780	0.779	0.861	0.883	0.831	0.838
	100	0.157	0.139	0.094	0.091	0.220	0.221	0.139	0.117	0.169	0.162
	n	*153*	*126*	*32*	*11*	*41*	*34*	*36*	*60*	*130*	*77*
*FH**	*115*	-	0.008	-	-	-	-	-	-	0.004	-
	100	0.752	0.726	0.797	0.750	0.758	0.734	0.729	0.795	0.721	0.767
	80	0.239	0.266	0.203	0.250	0.227	0.266	0.271	0.196	0.275	0.233
	65	0.010	-	-	-	0.015	-	-	0.009	-	-
	n	*153*	*126*	*32*	*10*	*33*	*32*	*35*	*56*	*120*	*75*
*GPI-A**	*150*	0.016	0.012	-	-	-	0.015	0.014	-	0.023	0.006
	140	-	0.004	-	-	-	-	-	0.008	0.004	-
	130	0.211	0.238	0.234	0.091	0.256	0.191	0.264	0.175	0.182	0.138
	125	0.003	0.012	0.016	-	-	0.015	-	-	0.004	-
	115	0.734	0.714	0.750	0.864	0.721	0.765	0.708	0.778	0.754	0.844
	100	0.023	0.012	-	0.045	0.012	-	0.014	0.024	0.027	0.006
	95	0.006	0.008	-	-	0.012	0.015	-	0.008	0.008	0.006
	90	0.006	-	-	-	-	-	-	0.008	-	-
	n	*154*	*126*	*32*	*11*	*43*	*34*	*36*	*63*	*132*	*80*
*GPI-B**	*140*	-	0.004	-	-	-	-	-	-	0.004	-
	120	0.060	0.080	0.109	0.091	0.060	0.132	0.059	0.098	0.044	0.063
	100	0.599	0.532	0.594	0.500	0.643	0.588	0.529	0.566	0.597	0.625
	80	0.341	0.380	0.297	0.409	0.298	0.279	0.412	0.328	0.355	0.313
	60	-	0.004	-	-	-	-	-	0.008	-	-
	n	*151*	*125*	*32*	*11*	*42*	*34*	*34*	*61*	*124*	*80*
*G3PDH-2**	*130*	0.003	0.015	-	-						
	100	0.500	0.550	0.552	0.591						
	75	0.487	0.431	0.431	0.409						
	65	0.010	0.005	0.017	-						
	n	*150*	*101*	*29*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*MPI**	*110*	0.127	0.374	0.143	0.250						
	100	0.853	0.626	0.810	0.667						
	90	0.020	-	0.048	0.083						
	n	*150*	*99*	*21*	*6*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*PGM-1**	*105*	0.142	0.130	0.121	0.200						
	100	0.594	0.710	0.552	0.500						
	95	0.247	0.136	0.328	0.300						
	90	0.017	0.025	-	-						
	n	*144*	*81*	*29*	*5*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*PGM-2**	*130*	0.007	0.004	-	0.045	0.013	0.015	-	0.009	-	-
	120	0.238	0.262	0.200	0.273	0.154	0.162	0.200	0.255	0.188	0.216
	100	0.732	0.714	0.733	0.636	0.833	0.794	0.714	0.718	0.796	0.764
	80	0.010	0.016	0.067	0.045	-	0.015	0.057	0.009	0.004	0.020
	65	0.013	0.004	-	-	-	0.015	0.029	0.009	0.012	-
	n	*149*	*124*	*30*	*11*	*39*	*34*	*35*	*55*	*125*	*74*

Table 7.13. continued.

Locus	allele	WA IV	STAS	NSW	SAFR	WA I	WA II	WA III	WA V	GAB	LHR
Invariant loci: Alleles and sample sizes											
*mAAT**	*-100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*ADH**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*ESTD**	*115*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*mIDHP**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*sIDHP**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*LDH-1**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*LDH-2**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*LDH-C**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*sMDH-1**	*110*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*sMDH-2**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*sMEP**	*x*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*PEP1-1**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*PGDH**	*100*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*PROT-1**	*x*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*PROT-2**	*x*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*
*sSOD**	*140*	*24*	*111*	*32*	*11*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*	*n.a.*

Table 7.14. Warty oreo. Summary allozyme statistics for the four samples in which all 25 loci were scored. Mean and standard deviation provided. Mean heterozygosity is Nei's (1978) unbiased estimate. % poly = the percentage of loci polymorphic, where the frequency of the most common allele is less than 0.95.

Sample	Sample size	No. alleles	% poly	Heterozygosity
Western Australia IV	64.5 ± 12.1	1.9 ± 0.3	32.0	0.133 ± 0.042
Tasmania	111.8 ± 1.9	2.0 ± 0.3	32.0	0.141 ± 0.043
New South Wales	31.2 ± 0.5	1.6 ± 0.2	32.0	0.132 ± 0.042
South Africa	10.5 ± 0.3	1.6 ± 0.2	32.0	0.148 ± 0.048

Table 7.15. Warty oreo. Composite mitochondrial DNA haplotypes, frequencies, sample sizes (n), haplotype (nucleon) diversities (h) and nucleotide diversities (n.d.). Restriction enzyme order *Bgl* I and *Eco* RI.

mtDNA haplotype	WA IV	GAB	STAS	NSW	LHR	SAFR
AF	0.911	0.833	0.847	0.969	0.957	0.818
BF	0.067	0.042	0.094	0.031	0.044	0.182
AC	–	0.042	0.024	–	–	–
CF	0.022	0.042	0.024	–	–	–
DF	–	0.042	–	–	–	–
AE	–	–	0.012	–	–	–
n	*45*	*24*	*85*	*32*	*23*	*11*
h	0.169	0.312	0.276	0.063	0.087	0.327
n.d.	0.0034	0.0061	0.0061	0.0010	0.0014	0.0052

Table 7.16. Warty oreo. Analyses of genetic differentiation. H_S = average Hardy-Weinberg expected heterozygosity (genetic diversity for mtDNA) per sample. G_{ST}= proportion of genetic variation attributable to inter-sample differentiation.

	Number of			Chi-square analysis		Genetic diversity analysis		
Loci	alleles	fish	H_S	$\chi 2$	P	G_{ST}	$G_{ST.null} \pm SD$	P
(a) Western Australia IV, southern Tasmania, and New South Wales (3 populations)								
*sAAT-2**	3	167	0.006	1.015	1.000	0.005	0.007 ± 0.005	0.657
*CK-A**	2	311	0.225	1.780	0.395	0.006	0.005 ± 0.006	0.247
*FH**	4	311	0.368	7.354	0.262	0.004	0.005 ± 0.006	0.386
*GPI-A**	8	312	0.410	9.721	0.774	0.001	0.005 ± 0.005	0.879
*GPI-B**	5	308	0.545	5.889	0.408	0.005	0.005 ± 0.004	0.398
*G3PDH-2**	4	280	0.512	5.160	0.520	0.003	0.006 ± 0.006	0.595
*MPI**	3	270	0.349	49.173	<0.001	0.061	0.007 ± 0.007	<0.001
*PGM-1**	4	254	0.533	13.692	0.032	0.020	0.006 ± 0.005	0.014
*PGM-2**	5	303	0.416	12.346	0.134	0.003	0.005 ± 0.005	0.530
mtDNA	5	162	0.166	5.167	0.810	0.020	0.015 ± 0.011	0.246
(b) Western Australia IV, southern Tasmania, New South Wales, and South Africa (4 populations)								
*sAAT-2**	3	178	0.005	1.214	1.000	0.005	0.010 ± 0.009	0.703
*CK-A**	2	322	0.210	2.276	0.527	0.008	0.013 ± 0.014	0.520
*FH**	4	321	0.370	7.710	0.456	0.003	0.014 ± 0.015	0.843
*GPI-A**	8	323	0.369	13.894	0.793	0.020	0.013 ± 0.010	0.172
*GPI-B**	5	319	0.552	7.988	0.623	0.007	0.013 ± 0.011	0.654
*G3PDH-2**	4	291	0.505	5.962	0.726	0.004	0.013 ± 0.013	0.805
*MPI**	3	276	0.383	52.079	<0.001	0.049	0.022 ± 0.022	0.103
*PGM-1**	4	259	0.555	14.667	0.101	0.022	0.024 ± 0.018	0.423
*PGM-2**	5	314	0.441	18.629	0.101	0.007	0.013 ± 0.012	0.601
mtDNA	5	173	0.199	7.239	0.842	0.033	0.030 ± 0.021	0.357
(c) Western Australia I-V (only WA IV for mtDNA), Great Australian Bight, southern Tasmania, New South Wales, Lord Howe Rise, South Africa (10 populations for allozymes, 6 for mtDNA)								
*CK-A**	2	700	0.254	9.824	0.332	0.014	0.011 ± 0.007	0.242
*FUM**	4	672	0.373	19.767	0.771	0.004	0.013 ± 0.007	0.965
*GPI-A**	8	711	0.373	49.184	0.861	0.015	0.011 ± 0.006	0.240
*GPI-B**	5	694	0.540	27.757	0.760	0.008	0.012 ± 0.006	0.685
*PGM-2**	5	676	0.395	52.596	0.058	0.013	0.012 ± 0.006	0.358
mtDNA	6	220	0.196	19.753	0.722	0.034	0.034 ± 0.017	0.404

Table 7.17. Warty oreo. Probabilities from chi-square analysis between pairs of samples for *MPI** allele frequencies. Values less than 0.05 are recorded, * indicates value significant after Bonferroni adjustment, n.s. = not significant.

	WA	**STAS**	**NSW**	**SAFR**
WA	–	<0.001*	n.s.	n.s.
STAS		–	0.002*	0.023
NSW			–	n.s.

Table 7.18. Warty oreo. Meristic data from six samples. See text for character abbreviations and Table 5.3 for sample details. (min = minimum count, max = maximum count, SD = standard deviation around mean, n = number of individuals for which character was scored)

Sample		DS	DR	DC	AS	AR	AC	LVS	LVR	RVS	RVR	LP	RP	LUGR	LMGR	LLGR	LTGR	RUGR	RMGR	RLGR	RTGR	LL	PC
WA	mean	6.24	29.37	35.62	2.75	27.41	30.16	1.01	5.92	1.00	5.97	18.69	18.65	4.79	1.00	18.58	23.71	4.76	1.00	18.79	23.81	90.30	8.33
	min	5	27	34	2	26	28	1	0	1	5	17	17	4	1	15	21	3	1	16	20	77	3
	max	7	31	37	3	30	32	2	6	1	6	21	21	7	1	21	27	6	1	22	27	105	10
	SD	0.49	0.78	0.67	0.43	0.75	0.72	0.10	0.53	0.00	0.16	0.74	0.72	0.64	0.00	1.29	1.46	0.62	0.00	1.25	1.45	5.16	0.78
	n	185	185	185	186	185	185	186	186	185	185	185	185	185	60	177	177	186	48	186	186	168	261
GAB	mean	6.09	29.46	35.56	2.56	27.48	30.00	1.00	6.00	1.00	6.00	18.63	18.47	4.73	1.00	18.96	23.76	4.54	1.00	18.84	23.40	84.52	8.29
	min	5	27	33	2	26	29	1	5	1	5	16	17	4	1	17	22	3	1	17	21	74	7
	max	7	31	37	3	30	31	1	7	1	7	20	20	6	1	22	27	5	1	22	26	102	11
	SD	0.35	0.87	0.79	0.50	0.88	0.73	0.00	0.19	0.00	0.19	0.70	0.71	0.57	0.00	1.18	1.29	0.57	0.00	1.13	1.22	4.76	0.78
	n	54	57	54	57	58	57	58	58	57	57	57	57	51	4	50	50	57	1	57	57	54	133
STAS	mean	6.30	29.31	35.61	2.79	27.37	30.17	1.00	5.93	1.00	5.91	18.49	18.55	4.72	1.00	18.71	23.48	4.80	1.00	18.51	23.36	86.84	8.33
	min	5	27	33	2	25	28	1	5	1	5	15	16	4	1	15	20	4	1	16	20	78	7
	max	8	31	37	4	29	31	1	6	1	6	20	20	6	1	22	26	6	1	21	26	96	11
	SD	0.55	0.96	0.83	0.45	0.93	0.76	0.00	0.26	0.00	0.28	0.78	0.78	0.55	0.00	1.29	1.34	0.50	0.00	1.18	1.29	4.81	0.84
	n	67	67	67	67	65	65	69	69	69	69	69	67	67	3	68	67	69	4	69	69	61	77
NSW	mean	6.48	29.07	35.53	2.97	26.83	29.80	1.00	5.97	1.00	6.00	18.48	18.42	4.91	1.00	18.90	23.97	5.00	1.00	19.10	24.19	86.50	8.00
	min	6	27	34	2	25	28	1	5	1	6	17	17	4	1	17	22	4	1	17	21	80	7
	max	7	32	39	4	29	32	1	6	1	6	20	20	6	1	21	21	6	1	21	26	98	9
	SD	0.51	0.85	0.98	0.32	0.83	0.85	0.00	0.18	0.00	0.00	0.63	0.67	0.54	0.00	0.91	1.11	0.52	0.00	1.03	1.20	5.06	0.68
	n	31	31	32	31	30	30	31	31	30	30	31	31	31	5	31	31	32	3	32	32	29	31
LHR	mean	6.20	29.00	35.07	2.70	27.28	29.98	1.00	5.95	1.00	5.83	18.43	18.32	4.77	1.00	18.71	23.71	4.87	1.00	18.64	23.70	87.77	8.12
	min	5	26	29	2	26	29	1	5	1	2	17	16	2	1	17	21	4	1	16	21	79	7
	max	7	32	38	3	29	32	1	6	1	6	20	20	6	1	32	27	6	1	22	28	105	11
	SD	0.49	0.89	1.22	0.46	0.69	0.59	0.00	0.23	0.00	0.64	0.72	0.78	0.70	0.00	1.46	1.51	0.52	0.00	1.30	1.20	4.91	0.72
	n	54	54	57	54	54	54	55	55	53	53	54	53	50	11	51	54	53	10	53	53	48	74
S Africa	mean	6.00	29.33	35.00	3.00	27.33	30.33	1.00	6.00	1.00	6.00	19.00	19.33	5.33	–	18.67	24.00	5.50	–	20.50	26.00	88.00	8.60
	min	6	29	35	3	27	30	1	6	1	6	18	19	5	–	18	24	5	–	20	25	88	8
	max	6	30	35	3	28	31	1	6	1	6	20	20	6	–	19	24	6	–	21	27	88	10
	SD	0.00	0.58	0.00	0.00	0.58	0.58	0.00	0.00	0.00	0.00	1.00	0.58	0.58	–	0.58	0.00	0.71	–	0.71	1.41	–	0.70
	n	2	3	2	3	3	3	3	3	2	2	3	3	3	0	3	3	2	0	2	2	1	10

Table 7.19. Warty oreo. Probabilities from chi-square analysis between pairs of samples for dorsal fin counts. Values less than 0.05 are recorded, * indicates value significant after Bonferroni adjustment, n.s. = not significant.

	WA	GAB	STAS	NSW	LHR
WA	–	n.s.	n.s.	n.s.	<0.001*
GAB		–	n.s.	n.s.	0.032
STAS			–	n.s.	0.009
NSW				–	n.s.

Table 7.20. Warty oreo. Correlations of pyloric cecae and lateral line scale counts with length. Note, correlations only given for samples with n>20.

				regression analysis			
sample	**n**	**mean length**	**mean count**	**intercept**	**slope**	**correlation coefficient**	***P***
Pyloric cecae							
GAB	187	19.192	8.187	7.321	0.045	0.183	0.012
LHR	75	19.113	8.093	7.252	0.044	0.253	0.028
NSW	30	24.380	8.000	7.967	0.001	0.004	0.982
STAS	74	22.953	8.284	8.359	-0.003	-0.016	0.890
WA	266	20.354	8.305	7.999	0.015	0.067	0.273
Lateral line scales							
GAB	54	18.981	84.519	75.567	0.472	0.276	0.044
LHR	48	19.810	87.771	81.126	0.335	0.270	0.063
NSW	27	24.144	86.593	61.867	1.024	0.408	0.034
STAS	48	20.219	86.625	82.405	0.209	0.159	0.282
WA	168	21.885	90.304	83.290	0.320	0.155	0.044

Table 7.21. Spikey oreo. Table of allele frequencies for 28 loci scored. n = number of individuals scored. na = locus not analysed for sample of fish. – = allele not detected.

Locus	Allele	WA	GAB	SA	WTAS	STAS	ETAS 1	ETAS 2	ETAS 3	BS	NSW	LHR	NZ
Variable loci													
*mAAT**	*100*	–	–	0.004	–	–	0.003	–	–	–	–	–	–
	0	0.007	–	0.004	–	0.011	0.009	0.017	–	–	0.009	0.005	0.005
	-100	0.885	0.896	0.912	0.916	0.922	0.884	0.852	0.871	0.833	0.881	0.892	0.839
	-200	0.108	0.104	0.079	0.084	0.067	0.104	0.126	0.129	0.167	0.110	0.102	0.156
	-250	–	–	–	–	–	–	0.004	–	–	–	–	–
	n	139	24	114	89	45	159	115	35	6	59	93	93
*sAAT-1**	*110*	0.267		0.285	0.238	0.239	0.259	0.243	0.081		0.276	0.247	0.207
	100	0.733		0.715	0.762	0.761	0.741	0.757	0.919		0.724	0.753	0.793
	n	105	na	100	86	44	133	70	31	na	49	85	75
*sAAT-2**	*125*	–		–	–		–	–			–	0.021	–
	120	–		–	–		0.005	–			–	–	–
	100	1.000		1.000	1.000		0.985	1.000			1.000	0.979	1.000
	80	–		–	–		0.010	–			–	–	–
	n	24	na	24	91	na	96	115	na	na	24	24	24
*CK-A**	*115*	–	–	–	–	–	–	–	–	–	–	0.005	–
	100	0.951	0.964	0.969	0.962	0.956	0.947	0.957	0.971	1.000	0.949	0.929	0.941
	90	0.049	0.036	0.026	0.038	0.044	0.053	0.043	0.029	–	0.051	0.066	0.059
	80	–	–	0.004	–	–	–	–	–	–	–	–	–
	n	144	28	114	91	45	159	115	35	6	59	98	93
*ESTD**	*100*	1.000		0.979	1.000		1.000	1.000			1.000	1.000	0.979
	85	–		0.021	–		–	–			–	–	0.021
	n	24	na	24	96	na	96	115	na	na	24	24	24

Table 7.21. continued.

Locus	Allele	WA	GAB	SA	WTAS	STAS	ETAS 1	ETAS 2	ETAS 3	BS	NSW	LHR	NZ
*FH**	*115*	–		0.013	0.005	–	0.006	0.004	0.014	–	0.009	0.005	0.011
	100	0.992		0.974	0.984	0.989	0.984	0.987	0.929	1.000	0.983	0.984	0.984
	80	0.008		0.013	0.011	0.011	0.009	0.009	0.057	–	0.009	0.010	0.005
	n	123		114	91	45	159	115	35	6	58	96	93
*GPI-1**	*130*	–	–	0.004	0.011	0.011	0.009	0.009	–	–	0.017	0.005	0.005
	125	0.010	0.017	0.004	0.022	0.022	0.028	0.004	0.043	–	0.009	0.005	0.005
	115	0.337	0.362	0.342	0.357	0.356	0.305	0.329	0.400	0.167	0.322	0.327	0.382
	100	0.628	0.586	0.627	0.566	0.556	0.626	0.632	0.529	0.750	0.610	0.633	0.581
	90	0.017	0.017	0.013	0.022	0.011	0.019	–	–	–	0.025	0.020	0.005
	85	0.007	0.017	0.009	0.022	0.044	0.013	0.026	0.029	–	0.017	0.010	0.016
	75	–	–	–	–	–	–	–	–	0.083	–	–	0.005
	n	144	29	114	91	45	159	114	35	6	59	98	93
*GPI-2**	*140*	0.003	–	0.004	–	–	0.003	0.004	–	–	0.017	–	0.005
	100	0.587	0.620	0.500	0.516	0.567	0.569	0.526	0.600	0.667	0.593	0.536	0.516
	80	0.410	0.380	0.496	0.478	0.433	0.428	0.470	0.400	0.333	0.390	0.464	0.478
	60	–	–	–	0.005	–	–	–	–	–	–	–	–
	n	144	25	113	91	45	159	115	35	6	59	98	93
*G3PDH-2**	*165*	–		–	0.006	–	–	0.004	–	–	–	0.005	–
	130	0.058		0.053	0.068	0.012	0.065	0.031	0.044	0.167	0.052	0.036	0.067
	100	0.901		0.890	0.858	0.965	0.892	0.925	0.912	0.833	0.897	0.918	0.883
	75	0.041		0.057	0.068	0.023	0.042	0.040	0.044	–	0.052	0.041	0.050
	n	121	na	114	88	43	153	113	34	6	58	98	90
*sIDHP**	*100*	0.979		1.000	1.000		1.000	1.000			0.979	1.000	1.000
	50	0.021		–	–		–	–			0.021	–	–
	n	24	na	24	91	na	96	115	na	na	24	48	72

Table 7.21. continued.

Locus	Allele	WA	GAB	SA	WTAS	STAS	ETAS 1	ETAS 2	ETAS 3	BS	NSW	LHR	NZ
*LDH-C**	*100*	0.979		1.000	0.995		1.000	1.000			1.000	0.979	1.000
	85	0.021		–	0.005		–	–			–	0.021	–
	n	24	na	24	91	na	96	115	na	na	24	96	24
*LDH-1**	*100*	1.000		1.000	1.000		1.000	1.000			0.979	1.000	1.000
	40	–		–	–		–	–			0.021	–	–
	n	24	na	24	91	na	96	115	na	na	24	24	24
*MPI**	*110*	0.106		0.083	0.047	0.012	0.035	0.049	–	–	0.026	0.063	–
	100	0.752		0.748	0.765	0.860	0.758	0.748	0.818	0.917	0.781	0.797	0.857
	90	0.128		0.170	0.188	0.128	0.207	0.199	0.182	0.083	0.193	0.141	0.143
	80	0.013		–	–	–	–	0.004	–	–	–	–	–
	n	113	na	109	85	43	157	113	33	6	57	96	91
*PEPB**	*100*	1.000		0.979	1.000		1.000	1.000			1.000	1.000	1.000
	85	–		0.021	–		–	–			–	–	–
	n	24	na	24	91	na	96	115	na	na	24	24	24
*PGDH**	*130*	0.004		–	–	–	–	–	–	–	–	–	–
	120	0.004		–	0.006	0.011	0.009	0.009	–	–	–	0.010	–
	110	0.147		0.208	0.202	0.211	0.192	0.148	0.186	0.250	0.153	0.193	0.213
	100	0.836		0.774	0.787	0.767	0.792	0.839	0.814	0.750	0.847	0.797	0.775
	90	0.008		0.018	0.006	0.011	0.006	0.004	–	–	–	–	0.013
	n	119	na	113	89	45	159	115	35	6	59	96	80

Table 7.21. continued.

Locus	Allele	WA	GAB	SA	WTAS	STAS	ETAS 1	ETAS 2	ETAS 3	BS	NSW	LHR	NZ
*PGM-1**	*115*	–		0.005	–	–	–	–	–	–	–	–	–
	110	–		0.014	–	–	0.003	–	0.015	–	0.017	–	–
	105	0.128		0.091	0.115	0.133	0.075	0.060	0.106	–	0.095	0.077	0.154
	100	0.593		0.636	0.563	0.544	0.632	0.619	0.636	0.833	0.672	0.655	0.505
	95	0.221		0.245	0.253	0.311	0.242	0.284	0.182	0.167	0.164	0.237	0.250
	90	0.058		0.009	0.069	0.011	0.038	0.037	0.030	–	0.052	0.031	0.090
	85	–		–	–	–	0.009	–	0.030	–	–	–	–
	n	113	na	110	87	45	159	109	33	6	58	97	94
*PGM-2**	*125*	–	–	–	0.005	–	0.003	–	–	–	–	–	0.005
	120	0.028	0.050	0.045	0.027	–	0.022	0.040	0.043	0.083	0.026	0.026	0.016
	100	0.930	0.825	0.920	0.940	0.956	0.940	0.884	0.929	0.833	0.939	0.923	0.943
	80	0.042	0.125	0.031	0.027	0.044	0.031	0.067	0.014	0.083	0.026	0.041	0.036
	65	–	–	0.004	–	–	0.003	0.009	0.014	–	0.009	0.010	–
	n	142	20	112	91	45	159	112	35	6	57	97	96
*sSOD**	*140*	0.862	0.768	0.243	0.099	0.644	0.129	0.164	0.914	0.833	0.949	0.663	0.768
	100	0.138	0.232	0.757	0.901	0.356	0.871	0.836	0.086	0.167	0.051	0.337	0.232
	n	141	28	113	91	45	159	113	35	6	59	98	95
Monomorphic loci													
*ADH**	*100*	24	na	24	91	na	96	115	na	na	24	24	24
*mIDHP**	*100*	24	na	24	91	na	96	115	na	na	24	24	24
*LDH-2**	*100*	24	na	24	91	na	96	115	na	na	24	24	24
*sMDH-1**	*100*	24	na	24	91	na	96	115	na	na	24	24	24
*sMDH-2**	*100*	24	na	24	91	na	96	115	na	na	24	24	24

Table 7.22. Spikey oreo. Summary statistics for the eight samples in which all 28 loci were scored. Mean and standard deviation provided. Mean heterozygosity is Nei's (1978) unbiased estimate. % poly = the percentage of loci polymorphic, where the frequency of the most common allele is less than 0.95.

Sample	Sample size	No. alleles	% poly	Heterozygosity
Western Australia	69.0 ± 10.2	2.0 ± 0.2	35.7	0.129 ± 0.035
South Australia	61.6 ± 8.4	2.1 ± 0.3	35.7	0.135 ± 0.036
Western Tasmania	90.4 ± 0.4	2.0 ± 0.3	35.7	0.128 ± 0.037
Eastern Tasmania 1	121.8 ± 5.8	2.2 ± 0.3	39.3	0.127 ± 0.035
Eastern Tasmania 2	112.8 ± 1.6	2.0 ± 0.3	35.7	0.128 ± 0.035
New South Wales	38.4± 3.2	2.0 ± 0.3	39.3	0.121 ± 0.034
Lord Howe Rise	58.2± 6.8	2.0 ± 0.2	39.3	0.134 ± 0.035
New Zealand	54.2± 6.3	2.0 ± 0.3	39.3	0.134 ± 0.037

Table 7.23. Spikey oreo. Observed and Hardy-Weinberg expected genotype distributions at the *sSOD** locus in the South Australian sample.

Genotype	*140/140*	*140/100*	*100/100*	Total
observed	14	27	72	113
expected	6.673	41.573	64.755	113

$\chi^2 = 14.385$, df = 1, $P < 0.001$

Table 7.24. Spikey oreo. Analyses of genetic differentiation. H_S = average Hardy-Weinberg expected heterozygosity (genetic diversity for mtDNA) per sample. G_{ST} = proportion of genetic variation attributable to inter-sample differentiation.

	Number of			Chi-square analysis		Genetic diversity analysis		
Loci	**alleles**	**fish**	H_S	$\chi 2$	P	G_{ST}	$G_{ST.null} \pm SD$	P
*mAAT**	5	941	0.203	28.561	0.797	0.006	0.006 ± 0.003	0.349
*sAAT-1**	2	778	0.323	13.314	0.140	0.017	0.007 ± 0.003	0.013
*CK-A**	4	953	0.089	21.741	0.710	0.003	0.006 ± 0.003	0.807
*FH**	3	929	0.041	19.730	0.341	0.013	0.006 ± 0.003	0.021
*GPI-A**	7	952	0.519	55.413	0.397	0.005	0.006 ± 0.003	0.619
*GPI-B**	4	952	0.496	25.880	0.507	0.005	0.006 ± 0.003	0.568
*G3PDH**	4	912	0.177	19.981	0.837	0.007	0.006 ± 0.002	0.341
*MPI**	4	898	0.347	66.375	< 0.001	0.010	0.006 ± 0.003	0.082
*PGDH**	5	910	0.320	28.018	0.814	0.005	0.006 ± 0.003	0.639
*PGM-1**	7	905	0.558	104.589	< 0.001	0.010	0.006 ± 0.002	0.055
*PGM-2**	5	946	0.132	30.600	0.741	0.005	0.006 ± 0.002	0.525
*sSOD**	2	949	0.280	825.643	< 0.001	0.436	0.006 ± 0.003	< 0.001
mtDNA	34	620	0.670	173.834	0.406	0.014	0.016 ± 0.005	0.557

Table 7.25. Spikey oreo. Probabilities from chi-square analysis (Roff and Bentzen 1989) of pairwise comparisons of *MPI** (above diagonal) and *PGM-1** (below diagonal). All chi-square analyses are based on 1000 randomizations. Probabilities less than 0.05 are given and those significant at 0.05 level after Bonferroni adjustment for multiple tests are in bold; probabilities greater than 0.05 are given as n.s. (not significant).

	WA	SA	WTAS	STAS	ETAS1	ETAS2	ETAS3	NSW	LHR	NZ
WA	–	n.s.	0.035	0.032	**<0.001**	0.026	0.034	0.015	n.s.	**<0.001**
SA	0.012	–	n.s.	0.027	0.039	n.s.	n.s.	n.s.	n.s.	**<0.001**
WTAS	n.s.	0.006	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.005
STAS	n.s.	n.s.	n.s.	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
ETAS1	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.	n.s.	n.s.	0.004
ETAS2	0.042	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.	n.s.	0.002
ETAS3	0.027	n.s.	0.040	n.s.	n.s.	0.018	–	n.s.	n.s.	n.s.
NSW	n.s.	n.s.	n.s.	0.027	n.s.	0.034	n.s.	–	n.s.	0.035
LHR	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	**0.001**
NZ	n.s.	**<0.001**	n.s.	n.s.	**<0.001**	**<0.001**	0.010	0.014	**0.001**	–

Table 7.26. Spikey oreo. Probabilities from chi-square analysis (Roff and Bentzen 1989) of pairwise comparisons of *sSOD**. All chi-square analyses are based on 1000 randomizations. Probabilities less than 0.05 are given and those significant at 0.05 level after Bonferroni adjustment for multiple tests are in bold; probabilities greater than 0.05 are given as n.s. (not significant).

	SA	WTAS	STAS	ETAS1	ETAS2	ETAS3	NSW	LHR	NZ	GAB
WA	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	n.s.	0.010	**<0.001**	0.013	n.s.
SA	–	**<0.001**	**<0.001**	**<0.001**	0.049	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
WTAS		–	**<0.001**	n.s.	0.049	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
STAS			–	**<0.001**	**<0.001**	**<0.001**	**<0.001**	n.s.	0.029	n.s.
ETAS1				–	n.s.	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
ETAS2					–	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
ETAS3						–	n.s.	**<0.001**	0.010	0.029
NSW							–	**<0.001**	**<0.001**	**<0.001**
LHR								–	0.034	n.s.
NZ									–	n.s.

Table 7.27. Spikey oreo. Observed and expected genotype distributions, given a 5:1 mix of shallow water and deep water groups, at the *sSOD** locus in the South Australian sample.

Genotype	***140/140***	***140/100***	***100/100***	**Total**
observed	14	27	72	113
expected	13.67	27.47	71.86	113

$\chi^2 = 0.016$, df = 1, $P = 0.899$

Table 7.28. Spikey oreo. Composite mitochondrial DNA haplotypes, frequencies, sample sizes, haplotype (nucleon) diversities (h) and nucleotide diversities (n.d.). Restriction enyme order *Apa* I and *Ava* I.

	WA	SA	WTAS	STAS	ETAS 1	ETAS 2	ETAS 3	NSW	LHR	NZ
AA	0.404	0.433	0.444	0.400	0.392	0.388	0.314	0.310	0.316	0.368
AB	0.500	0.433	0.367	0.333	0.405	0.367	0.286	0.414	0.379	0.439
BA	0.058	0.067	0.133	0.156	0.139	0.184	0.257	0.207	0.179	0.140
CA	0.019	0.017	0.011	0.022	–	0.020	0.029	0.034	0.032	0.018
AC	–	–	0.022	–	–	–	–	–	0.011	–
AE	–	–	–	–	–	–	–	–	0.011	–
BB	–	–	0.022	–	0.026	–	–	–	0.042	–
DB	0.019	0.017	–	0.044	–	0.020	0.057	–	0.011	–
KA	–	–	–	–	–	–	–	–	0.011	–
EA	–	–	–	–	–	–	–	–	0.011	–
MA	–	–	–	–	–	–	–	0.017	–	–
DD	–	–	–	0.022	–	–	0.029	0.017	–	–
DA	–	0.017	–	–	0.013	–	–	–	–	0.018
DC	–	0.017	–	–	–	–	–	–	–	–
JB	–	–	–	–	0.013	–	–	–	–	–
FA	–	–	–	–	0.013	–	–	–	–	–
GA	–	–	–	–	–	0.020	–	–	–	–
LB	–	–	–	–	–	–	0.029	–	–	–
NB	–	–	–	0.022	–	–	–	–	–	–
OA	–	–	–	–	–	–	–	–	–	0.018
n	*52*	*60*	*90*	*45*	*79*	*49*	*35*	*58*	*95*	*57*
h	0.594	0.629	0.656	0.717	0.670	0.694	0.770	0.700	0.733	0.663
n.d.	0.0086	0.0098	0.0100	0.0124	0.0108	0.0115	0.0184	0.0140	0.0129	0.0107

Table 7.29. Spikey oreo. Composite mitochondrial DNA haplotype frequencies of the ND5/ND6 region of the molecule digested by *Hin* PI and *Sty* I, with sample sizes, and haplotype (nucleon) diversities (h)

	'Deep'		'Shallow'
Haplotype	**TAS 3**	**LHR**	**ETAS 2**
AB	0.036	–	–
BA	–	0.063	0.033
BB	0.286	0.375	0.433
CA	0.500	0.531	0.467
CB	0.036	–	–
AA	0.143	0.031	0.067
n	*28*	*32*	*30*
h	0.669	0.591	0.609

Table 7.30. Spikey oreo. Meristic data from twelve samples. See text for character abbreviations and Table 5.4 for sample details. (min = minimum count, max - maximum count, SD = standard deviation around mean, n = number of individuals for which character was scored).

Sample		DS	DR	DC	AS	AR	AC	LVS	LVR	RVS	RVR	LP	RP	LUGR	LMGR	LLGR	LTGR	RUGR	RMGR	RLGR	RTGR	LL	PC
	mean	7.27	32.82	40.10	3.59	30.86	34.45	1.00	5.96	1.00	5.98	20.16	20.22	4.70	1.00	17.58	22.56	4.82	1.00	17.80	22.88	106.10	11.09
	min	6	30	38	3	28	32	1	5	1	5	19	18	3	1	15	20	3	1	16	21	97	9
WA	max	8	35	42	4	33	36	1	6	1	6	22	22	6	1	20	26	6	1	20	25	115	13
	SD	0.53	0.95	0.85	0.50	0.92	0.86	0.00	0.20	0.00	0.14	0.69	0.86	0.54	0.00	1.01	1.28	0.56	0.00	0.98	1.03	4.66	0.98
	n	51	51	51	51	51	51	51	51	50	50	49	51	50	14	50	50	51	13	51	51	49	81
	mean	7.44	32.58	40.02	3.84	30.42	34.26	1.00	5.86	1.00	5.90	20.31	20.18	4.93	1.00	18.26	23.49	4.98	1.00	17.96	23.02	104.96	11.07
	min	7	31	39	3	29	33	1	5	1	4	17	17	4	1	16	21	4	1	16	20	94	9
SA	max	8	35	42	4	32	36	1	6	1	6	22	22	6	1	20	26	6	1	21	27	116	13
	SD	0.50	0.86	0.65	0.37	0.78	0.72	0.00	0.35	0.00	0.37	0.82	0.85	0.51	0.00	0.90	1.20	0.52	0.00	1.02	1.23	5.13	0.96
	n	50	50	50	50	50	50	50	49	49	49	49	50	43	13	43	43	49	4	49	49	46	100
	mean	7.10	32.97	40.07	3.62	30.78	34.40	1.00	5.93	1.00	5.92	19.95	20.05	4.93	1.00	17.60	22.72	4.93	1.00	17.68	22.73	104.36	11.23
	min	6	31	39	3	28	32	1	3	1	4	18	19	4	1	15	20	4	1	16	20	91	9
WTAS	max	8	35	42	4	33	36	1	6	1	6	21	21	6	1	20	26	6	1	20	26	119	14
	SD	0.57	0.78	0.76	0.49	0.88	0.76	0.00	0.41	0.00	0.33	0.75	0.63	0.49	0.00	1.08	1.37	0.32	0.00	1.05	1.27	5.18	1.12
	n	60	60	60	60	60	60	60	60	60	60	60	58	59	10	58	58	57	7	56	56	58	91
	mean	7.30	32.68	39.98	3.82	30.40	34.22	1.00	5.93	1.00	5.93	20.33	20.40	5.05	1.00	17.91	23.18	4.96	1.00	18.25	23.39	104.56	10.81
	min	6	31	39	3	29	33	1	5	1	4	19	19	4	1	16	21	4	1	16	21	94	9
STAS	max	8	34	42	4	32	35	1	7	1	7	22	23	6	1	21	27	6	1	21	27	117	13
	SD	0.55	0.77	0.66	0.39	0.69	0.56	0.00	0.33	0.00	0.39	0.74	0.82	0.61	0.00	1.03	1.24	0.56	0.00	1.16	1.38	5.07	1.14
	n	44	44	44	45	45	45	45	45	45	45	45	43	44	10	44	44	45	8	44	44	45	36
	mean	7.05	32.95	40.00	3.53	31.02	34.55	1.00	5.93	1.00	5.86	20.31	20.20	4.93	1.00	18.07	23.18	4.67	1.00	18.07	22.84	106.57	11.43
	min	6	31	38	3	30	33	1	5	1	5	19	16	4	1	15	20	4	1	15	19	95	9
ETAS 1	max	8	35	43	4	33	36	1	6	1	6	22	22	6	1	21	26	6	1	21	26	120	14
	SD	0.51	0.93	0.91	0.50	0.82	0.81	0.00	0.26	0.00	0.35	0.70	0.93	0.56	0.00	1.27	1.49	0.64	0.00	1.17	1.52	5.02	1.13
	n	57	57	57	57	56	56	55	55	57	57	54	55	57	10	57	57	55	5	55	55	56	155
	mean	7.11	32.95	40.06	3.60	30.80	34.39	1.00	5.98	1.00	6.00	20.31	20.23	5.02	1.00	18.07	23.35	5.04	1.00	18.22	23.40	104.75	10.60
	min	6	31	39	3	29	33	1	5	1	5	17	18	4	1	16	21	4	1	16	20	89	8
ETAS 2	max	8	35	41	4	33	36	1	7	1	7	23	23	6	1	20	26	7	1	22	27	114	13
	SD	0.46	0.83	0.74	0.49	0.99	0.88	0.00	0.24	0.00	0.19	1.00	1.03	0.41	0.00	1.17	1.36	0.58	0.00	1.11	1.38	5.87	1.22
	n	55	55	55	55	55	55	55	55	55	55	55	55	55	14	55	55	55	8	55	55	52	110

Table 7.30. continued.

Sample		DS	DR	CD	AS	AR	CA	LVS	LVR	RVS	RVR	LP	RP	LUGR	LMGR	LLGR	LTGR	RUGR	RMGR	RLGR	RTGR	LL	PC
	mean	7.31	32.57	39.89	3.69	30.66	34.34	1.00	5.86	1.00	5.89	20.31	20.44	5.09	1.00	17.97	23.20	5.09	1.00	17.71	22.94	107.46	10.47
	min	7	31	39	3	29	33	1	5	1	5	19	19	4	1	15	20	4	1	15	20	97	9
ETas 3	max	8	34	42	4	32	36	1	6	1	6	22	23	6	1	21	26	6	1	20	26	116	13
	SD	0.47	0.85	0.68	0.47	0.91	0.84	0.00	0.36	0.00	0.32	0.74	0.82	0.56	0.00	1.40	1.39	0.51	0.00	1.32	1.55	5.21	0.99
	n	35	35	35	35	35	35	35	35	35	35	32	34	35	5	35	35	35	5	35	35	35	34
	mean	7.00	32.83	39.83	4.00	30.00	34.00	1.00	5.83	1.00	6.00	20.20	20.00	5.00	1.00	17.33	22.50	5.00	1.00	18.17	23.50	106.67	10.67
	min	7	32	39	4	29	33	1	5	1	6	19	19	5	1	16	21	5	1	17	22	93	9
BS	max	7	34	41	4	31	35	1	6	1	6	21	21	5	1	19	25	5	1	20	26	115	13
	SD	0.00	0.75	0.75	0.00	0.89	0.89	0.00	0.41	0.00	0.00	0.84	0.89	0.00	–	1.03	1.38	0.00	0.00	1.17	1.52	8.36	1.53
	n	6	6	6	6	6	6	6	6	6	6	5	6	6	1	6	6	6	2	6	6	6	6
	mean	7.44	32.44	39.89	3.56	30.67	34.22	1.00	6.00	1.00	6.00	20.56	20.33	5.00	1.00	18.22	23.33	4.89	1.00	17.44	22.56	106.00	10.67
	min	7	31	39	3	29	33	1	6	1	6	20	20	5	1	17	22	4	1	16	20	97	9
NSW 1	max	8	33	41	4	32	35	1	6	1	6	22	21	5	1	19	24	6	1	19	25	116	13
	SD	0.53	0.73	0.60	0.53	0.87	0.67	0.00	0.00	0.00	0.00	0.88	0.50	0.00	–	0.67	0.71	0.60	0.00	1.24	1.51	6.32	1.32
	n	9	9	9	9	9	9	9	9	9	9	9	9	9	1	9	9	9	2	9	9	9	9
	mean	7.22	32.64	39.86	3.54	30.68	34.22	1.00	5.92	1.00	5.96	20.46	20.57	5.22	–	17.43	22.65	5.02	–	17.54	22.56	109.32	10.66
	min	6	31	38	3	29	33	1	5	1	5	18	19	4	–	15	20	4	–	14	19	100	8
NSW 2	max	8	34	42	4	33	36	1	6	1	6	22	22	6	–	21	27	6	–	21	26	121	12
	SD	0.55	0.72	0.76	0.50	0.89	0.79	0.00	0.28	0.00	0.20	0.76	0.76	0.47	–	1.29	1.49	0.55	–	1.33	1.49	4.84	1.08
	n	50	50	50	50	50	50	49	49	50	50	50	49	49	0	49	49	50	0	50	50	50	50
	mean	7.22	32.74	39.96	3.70	30.62	34.32	1.00	5.94	1.00	5.94	20.25	20.23	4.96	1.00	18.17	23.25	4.86	1.00	17.88	22.84	106.49	10.71
	min	6	31	39	3	29	33	1	5	1	5	19	19	4	1	15	19	4	1	15	19	97	9
LHR	max	8	35	42	4	33	36	1	6	1	6	22	21	6	1	22	27	6	1	22	26	118	14
	SD	0.55	1.05	0.86	0.46	0.81	0.77	0.00	0.24	0.00	0.24	0.86	0.69	0.46	0.00	1.17	1.45	0.54	0.00	1.38	1.53	5.05	1.35
	n	50	50	50	50	50	50	49	49	48	48	48	48	48	6	48	48	49	5	49	49	45	42
	mean	7.55	32.18	39.73	3.45	30.64	34.09	1.00	5.82	1.00	5.90	20.00	20.30	5.18	–	18.00	23.18	5.10	–	18.40	23.50	104.78	10.91
	min	7	31	38	3	30	33	1	5	1	5	18	19	5	–	16	21	5	–	17	22	97	10
NZ	max	10	33	41	4	32	35	1	6	1	6	22	22	6	–	21	27	6	–	20	25	112	13
	SD	0.93	0.87	0.79	0.52	0.67	0.70	0.00	0.40	0.00	0.32	1.18	0.82	0.40	–	1.34	1.66	0.32	–	1.17	1.27	4.99	1.04
	n	11	11	11	11	11	11	11	11	10	10	11	10	11	0	11	11	10	0	10	10	9	11

Table 7.31. Spikey oreo. Correlations of pyloric cecae and lateral line scale counts with length. Note, correlations only given for samples with n>20.

sample	n	mean length	mean count	regression analysis			
				intercept	slope	correlation coefficient	*P*
Pyloric caeca							
ETAS 1	155	26.372	11.426	9.075	0.089	0.220	0.006
ETAS 2	110	28.077	10.600	12.202	-0.057	-0.097	0.315
ETAS 3	34	31.212	10.471	10.338	0.004	0.013	0.941
GAB	38	19.589	10.605	11.268	-0.034	-0.130	0.437
LHR	54	30.650	10.574	8.974	0.052	0.326	0.016
SA	100	29.379	11.070	8.491	0.088	0.181	0.071
NSW 2	50	32.776	10.660	8.689	0.060	0.134	0.352
STAS	37	30.716	10.919	7.939	0.097	0.185	0.273
WA	82	23.238	11.085	10.766	0.014	0.066	0.555
WTAS	91	25.993	11.231	8.895	0.090	0.218	0.038
Lateral line scales							
ETAS 1	56	26.300	106.571	97.754	0.335	0.188	0.166
ETAS 2	52	28.019	104.750	83.944	0.743	0.289	0.037
ETAS 3	35	31.220	107.457	96.689	0.345	0.200	0.250
LHR	45	32.378	106.489	99.887	0.204	0.192	0.206
SA	46	29.752	104.957	86.744	0.612	0.266	0.074
SNSW	50	32.776	109.320	94.349	0.457	0.228	0.112
STAS	45	30.767	104.556	98.676	0.191	0.098	0.524
WA	49	25.137	106.102	92.295	0.549	0.326	0.022
WTAS	58	26.031	104.362	99.091	0.203	0.106	0.429

Table 7.32. Spikey oreo. Numbers of fish of each of the *sSOD** genotypes used for morphometric analysis. Note that only the two homozygous genotypes were used for the ANOVAs, but all fish were used for the canonical variate analyses.

Location	*sSOD*140/140*	*sSOD*140/100*	*sSOD*100/100*	Totals
Bass	4	2	0	6
ETas 1	1	10	10	21
E Tas 2	2	10	10	22
E Tas 3	10	4	1	15
S Tas	10	11	6	27
W Tas	0	10	10	20
LHR	10	10	5	25
NSW	10	4	1	15
NZ	8	3	0	11
SA	10	10	10	30
WA	10	10	2	22
Totals	75	84	55	214

Table 7.33. Spikey oreo. ß values obtained from the regression model ln(variable)=constant+ln(standard length+genotype.

Variable	HL	BD	DBL	ABL	OD	LW	UJ	LJ	PV
beta value	0.926	0.862	0.930	0.893	0.890	1.261	0.988	0.993	0.890

Variable	PA	CPD	CPL	SnLH
beta value	0.872	0.757	1.080	1.138

Table 7.34. Spikey oreo. Univariate and multivariate analyses of morphometric variation.

(a) Univariate analyses

	stock				genotype				interaction			
Variable	**DF**	**MS**	***F***	***P***	**DF**	**MS**	***F***	***P***	**DF**	**MS**	***F***	***P***
HL	9	124.555	3.611	0.001	1	86.592	2.510	0.116	7	26.962	0.779	0.607
Error	107	34.497			107	34.497			88	34.563		
BD	9	236.643	2.514	0.012	1	1.215	0.013	0.910	7	82.866	0.865	0.538
Error	107	94.132			107	94.132			88	95.844		
DBL	9	59.976	2.066	0.039	1	5.547	0.191	0.663	7	40.359	1.284	0.268
Error	107	29.031			107	29.031			88	31.431		
ABL	9	76.000	2.909	0.004	1	7.704	0.295	0.588	7	88.128	4.170	0.001
Error	107	26.121			107	26.121			88	21.136		
OD	9	94.871	5.376	0.000	1	1.060	0.060	0.807	7	9.479	0.531	0.809
Error	107	17.646			107	17.646			88	17.842		
LW	9	2.060	1.073	0.389	1	0.641	0.334	0.565	7	0.706	0.335	0.936
Error	107	1.920			107	1.920			88	2.107		
UJ	9	26.744	2.300	0.021	1	33.493	2.881	0.093	7	4.185	0.351	0.928
Error	107	11.627			107	11.627			88	11.918		
LJ	9	10.432	0.787	0.629	1	13.379	1.009	0.317	7	4.423	0.298	0.953
Error	107	13.260			107	13.260			88	14.858		
PV	9	60.063	1.925	0.056	1	5.628	0.180	0.672	7	17.297	0.534	0.807
Error	107	31.195			107	31.195			88	32.403		
PA	9	61.554	1.516	0.151	1	1.547	0.038	0.846	7	9.107	0.207	0.983
Error	107	40.600			107	40.600			88	43.945		
CPD	9	4.223	1.620	0.119	1	0.704	0.270	0.604	7	1.747	0.710	0.663
Error	107	2.607			107	2.607			88	2.459		
CPL	9	29.783	2.726	0.007	1	17.107	1.566	0.214	7	14.366	1.330	0.246
Error	107	10.926			107	10.926			88	10.801		
SnLH	9	36.226	1.683	0.102	1	0.039	0.002	0.966	7	22.656	0.985	0.448
Error	107	21.530			107	21.530			88	23.008		

(b) Multivariate analyses

	stock			genotype			interaction		
		DF	***P***		**DF**	***P***		**DF**	***P***
Wilk's Lambda=	0.153			0.838		0.316			
F-Statistic=	1.764	117,723	<0.001	1.411	13, 95	0.169	1.075	91,482	0.314
Pillai Trace=	1.516			0.162			0.997		
F-Statistic=	1.604	117,927	<0.001	1.411	13, 95	0.169	1.047	91,574	0.371
Hotelling-Lawley Trace=	2.429			0.193			1.350		
F-Statistic=	1.935	117,839	<0.001	1.411	13, 95	0.169	1.102	91,520	0.259

8. BENEFITS

Oreos are an important component of the South East Fishery and may eventually need to be managed as quota species. Thus determination of species composition and stock structure are basic to any future research or management plans for these species.

The recorded catches of individual oreo species in the SEF have been unreliable in the past due to confusion over species identification in catch log-books. Improved identification and more accurate recording of catches should now be possible using the information recorded in this Report. This should lead to improved knowledge of the biology and distribution of each of the species.

Similarly we now have an indication of the pattern of stock structure of Australasian oroes. The deep sea fishing fleet will benefit from this research by being provided with better management advice from management authorities. This better advice, coming from an improved stock assessment database will assist the setting of quotas or exploitation rates at levels commensurate with ecologically sustainable levels. From data obtained herein it may be possible to detect where additional stocks of species may exist or alternatively where they are unlikely to occur.

The conservation of biodiversity, both in terms of numbers of species and the genetic diversity contained within them, is a central tenet of the Commonwealth's Ecologically Sustainable Development strategy. Fishing activities can affect species compositions of exploited communities, either directly (by differentially removing targeted species) or indirectly (by, for example, trawling affecting the structure of epibenthic communities). Fishing activities could also be affecting the genetic diversity of exploited fishes. This study provides important baseline information on the levels of genetic diversity in relatively unexploited stocks of commercial oreo species, and it will be important to establish whether fishing pressures do impact on genetic diversity by monitoring levels of genetic diversity as exploitation continues. Such information will be of considerable interest to fisheries worldwide.

This report provides a review of biological and fisheries information on Australasian oreos which will be useful in planning future research.

9. INTELLECTUAL PROPERTY

No commercial intellectual property arose from this work.

10. FURTHER DEVELOPMENT

Our knowledge of the genetic basis of oreo stock structure could be improved in several ways. The most obvious is to increase the number of fish examined, both by analysing additional fish from areas already sampled, and by analysing fish from new areas. The analysis of additional fish will increase statistical power. These fish should be analysed for both allozyme and mitochondrial DNA variation. Existing allozyme techniques are perfectly acceptable, but thought should be given to detecting additional mtDNA variants. This goal would be most readily attained using PCR techniques to amplify known sequences of mtDNA, and then using 4-base cutters to digest these fragments. This approach was adopted towards the end of the present project in the examination of deep and shallow water spikey oreos.

The spikey oreo findings could be followed up by a depth-stratified sampling program to ascertain more precisely the distributions of two groups of fish we have termed races.

These genetic approaches should be supplemented with an examination of DNA microsatellite loci. These loci constitute a new class of recently discovered genetic markers. They comprise short one to four nucleotide repeats that are generally less than 300bp in total, but can be much larger (Tautz, 1989). Mutation rates are high, estimated at around 0.2% to 0.05% (Huang *et al.*, 1992; Kwiatkowski *et al.*, 1992), and heterozygosity high. This high mutation rate and high variability suggests that these markers may be more powerful than allozyme and mtDNA markers for stock delineation studies, although at present few comparative studies are available. Their promise was supported by one of the first studies of microsatellite variability in fish, which showed highly significant differences in allele frequencies at several microsatellite loci in samples of Atlantic cod off eastern Canada, whereas allozymes and mtDNA reveal little differentiation among local populations (Wright and Bentzen, 1994). The problem with microsatellite loci is that for each new group of fish examined, new markers have to be developed in a process that might take several months before the markers can be applied in a stock structure analysis. Nonetheless, the apparently increased power of the technique means that this investment is likely to be worthwhile.

Perhaps the most promising non-genetic approach to stock structure in deepwater species (which cannot be easily tagged) is that of otolith microchemistry analysis, especially of the primordium region. This approach has recently been applied to orange roughy (Anon. 1995c). While the resulting data were limited and could not be unequivocally interpreted, the general approach appeared to be useful. The standard caveat for such traits with unknown genetic and environmental aetiology applies: differences between samples of adults might reflect differences in age structure rather than true stock differences.

11. STAFF

STAFF WORKING ON THIS PROJECT AND THEIR MAJOR ROLES:

Bob Ward	CSOF7	Joint Principal Investigator - genetics
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13. REFERENCES

Abe, T. (1957). Note on fishes from the stomachs of whales taken in the Antarctic I. *Xenocyttus nemotoi*, a new genus and new species of zeomorph fish of the subfamily *Oreosominae* Goode and Bean, 1895. *Science Report Whales Research Institute* 12, 225–233.

Annala, J.H. (Comp.) (1995). Report from the Fishery Assessment Plenary, May 1995: stock assessments and yield estimates. 277p. (Unpublished report held in MAF Fisheries Greta Point library, Wellington, New Zealand).

Anon. (1994). MAF Fisheries New Zealand Marine Research Annual Report for 1993-1994.

Anon. (1995a). 'Marketing Names for Fish and Seafood in Australia'. Commonwealth of Australia, Canberra.

Anon. (1995b). Catch Watch-South East Fishery. *Australian Fisheries* 54 (3), 12-13.

Anon. (1995c) 'Trial Studies of Alternative Techniques for Stock Delineation of Orange Roughy'. FRRF Project 1992/93 #18. Final Report to the Australian Fisheries Management Authority

Avise, J.C. (1987). Identification and interpretation of mitochondrial DNA stocks in marine species. In, 'Proceedings of the Stock Identification Workshop'. (Ed H.E.Kumpf) pp 105-136. NOAA Technical Memorandum NMFS-SEFC-199, US Department of Commerce.

Beverton, R.J.H. (1990). Small pelagic fish and the threat of fishing; are they endangered? *Journal of Fish Biology* 37, 5-16.

Birky, C.W., Fuerst, P., and Maruyama, T. (1989). Organelle gene diversity under migration, mutation, and drift: equilibrium expectations, approach to equilibrium, effects of heteroplasmic cells, and comparison to nuclear genes. *Genetics* 121, 613-627.

Bolch, C.J.S., Elliott, N.G., and Ward, R.D. (1993). Enzyme variation in south-eastern Australian populations of the blue-eye or deepsea trevalla, *Hyperoglyphe antarctica* Carmichael 1818 (Teleostei: Stromateoidei). *Australian Journal of Marine and Freshwater Research* 44, 687-697.

Brasher, D.J., Ovenden, J.R., Booth, J.D., and White. R.W.G. (1992). Genetic subdivision of Australian and New Zealand populations of *Jasus verreauxi* (Decapoda: Palinuridae) - preliminary evidence from the mitochondrial genome. *New Zealand Journal of Marine and Freshwater Research* 26, 53-58.

Brown, W.M., George, M., and Wilson, A.C. (1979). Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Science USA* 76, 1967-1971.

Carvalho, G.R., and Hauser, L. (1994). Molecular genetics and the stock concept in fisheries. *Reviews in Fish Biology and Fisheries* 4, 326-350.

Chow, S., and Inoue, S. (1993). Intra- and interspecific restriction fragment length polymorphism in mitochondrial genes of *Thunnus* tuna species. *Bulletin of the National Research Institute of Far Seas Fisheries* 30, 207–225.

Collett, R. (1889). Diagnoses de poissons nouveaux provenant des campagnes de 'l'Hirondelle'. *Bulletin de la Société zoologique de France* 14, 306.

Cuvier, G. (1829). In Cuvier, G. and Valenciennes, M. (1829). 'Histoire Naturelle des Poissons' 4. Paris.

Doonan, I.J., McMillan, P.J., Coburn, R.P., Hart, A.C., and Cordue, P.L. (1995). Assessment of smooth oreo for 1995. New Zealand Fisheries Assessment Research Document 95/12, Ministry of Fisheries, Wellington, New Zealand.

Elliott, N.G., and Ward, R.D. (1992). Enzyme variation in orange roughy, *Hoplostethus atlanticus* (Teleostei: Trachichthyidae), from southern Australian and New Zealand waters. *Australian Journal of Marine and Freshwater Research* 43, 1561-1571.

Elliott, N.G., and Ward, R.D. (1994). Enzyme variation in jackass morwong, *Nemadactylus macropterus* (Schneider, 1801) (Teleostei: Cheilodactylidae), from Australian and New Zealand waters. *Australian Journal of Marine and Freshwater Research,* 45, 51-67.

Elliott, N.G., and Ward, R.D. (1995). Genetic relationships of eight species of Pacific tunas (Teleostei, Scombridae) inferred from allozyme analysis. *Marine and Freshwater Research* 46, 1021-1032.

Elliott, N.G., Smolenski, A.J., and Ward, R.D. (1994). Allozyme and mitochondrial DNA variation in orange roughy (*Hoplostethus atlanticus*): little differentiation between Australian and North Atlantic populations. *Marine Biology* 119, 621-627.

Farris, J.S. (1972). Estimating phylogenetic trees from distance matrices. *American Naturalist* 106, 645–668.

Fenton, G.E., Short, S.A., and Ritz, D.A. (1991). Age determination of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) using 210Pb:226Ra disequilibria. *Marine Biology* 109, 197–202.

Gilchrist, J. (1904). Descriptions of new South African fishes. *Marine Investigations, South Africa* 3, 1-16.

Gilchrist, J. (1906). Description of fifteen new South African fishes with notes on other species. *Marine Investigations, South Africa* 4, 143–171.

Gomon, M.F., Glover, C.J.M., and Kuiter, R.H. (1994). 'The Fishes of Australia's South Coast'. State Printers, Adelaide. 992pp

Greenwood P,H., Rosen, D.E., Weitzman, S.H., and Myers, G.S. (1966). Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* 131, 339-456.

Grewe, P.M., Krueger, C.C., Aquadro, C.F., Bermingham, E., Kincaid, H.L., and May, B. (1993). Mitochondrial DNA variation among lake trout (*Salvelinus namaycush*) strains stocked into Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 50, 2397–2403.

Grewe, P.M., Smolenski, A.J., and Ward, R.D. (1994). Mitochondrial DNA diversity in jackass morwong (*Nemadactylus macropterus*: Teleostei) from Australian and New Zealand waters. *Canadian Journal of Fisheries and Aquatic Sciences* 51, 1101-1109.

Hebert, P.D.N., and Beaton, M.J. (1989). 'Methodologies for allozyme analysis using cellulose acetate electrophoresis'. Helena Laboratories, Beaumont, Texas.

Heemstra, P.C. (1990). 'Oreosomatidae' in 'Fishes of the Southern Ocean' (Gon, O. and Heemstra, P.C. eds). JLB Smith Institute of Ichthyology, Grahamstown.

Holt, E. and Byrne, L. (1908). New deep-sea fishes from the south-west coast of Ireland. *Annals and Magazine of Natural History* (8)1, 86–95.

Huang, T., Cottingham, Jr., R., Ledbetter, D., and Zoghbi, H. (1992). Genetic mapping of four dinucleotide repeat loci, DXS453, DXS458, DXS454, and DXS424 on the X chromosome using multiplex polymerase chain reaction. *Genomics* 13, 375-380.

Hubbs, C.L., and Lagler, K.F. (1958). 'Fishes of the Great Lakes Region'. University of Michigan Press.

Hulme, T. J. (1995). The use of vertebral counts to discriminate between North Sea herring stocks. *ICES Journal of Marine Science* 52, 775-779.

Ihssen, P.E., Booke H.E., Casselman, J.M., McGlade, J.M., Payne, N.R., and Utter, F.M. (1981). Stock identification: materials and methods. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1838-1855.

James, G. D. (1984). Oreosomatidae. In, 'FAO Species Identification Sheets for Fishery Purposes. Western Indian Ocean (Fishing Area 51)', (eds. Fischer, W. and Bianchi, G). Prepared and printed with the support of the Danish International Development Agency (DANIDA). Vol. 3. Food and Agriculture Organization of the United Nations, Rome.

James, G.D., Inada, T., and Nakamura, I. (1988). Revision of the oreosomatid fishes (Family Oreosomatidae) from the southern oceans, with a description of a new species. *New Zealand Journal of Zoology* 15, 291-326.

Johnson, G.D., and Patterson, C. (1993). Percomorph pylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science* 52, 554-626.

Kailola, P.J., Williams, M.J., Stewart, P.C., Reichelt, R.E., McNee, A., and Grieve, C. (1993). 'Australian Fisheries Resources'. Bureau of Resource Sciences and Fisheries Research and Development Corporation. Canberra. 422 pp.

Karrer, C. (1990). Oreomatidae. In, 'Checklist of the Fishes of the Eastern Tropical Atlantic' (eds. J.C. Quero, J.C. Aureau, C. Karrer, A. Post & L. Saldonka). Vol. 2, 637-640

Keiser, T. (1984). DNAGEL: a computer program for determining DNA fragment sizes using a small computer equipped with a graphics tablet. *Nucleic Acid Research* 12, 670–688

Kocher, T.D., Thomas, W.K., Mayer, A., Edwards, S.V., Paabo, S., Villablanca, F.X., and Wilson, A.C. (1989). Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences USA* 86, 6196-6200.

Kwiatkowski, D., Henske, E., Weimer, K., Ozelius, J., Gusella, J., and Haines, J. (1992). Construction of a GT polymorphism map of human 9q. *Genomics* 12, 229-240.

Lacépede, B.G.E. (1802). 'Histoire Naturelle des Poissons'. Vol. 4, i-xliv+1-728.

Lessios, H.A. (1992). Testing electrophoretic data for agreement with Hardy-Weinberg expectations. *Marine Biology* 112, 517-523.

Levene, H. (1949). On a matching problem arising in genetics. *Annals of Mathematics and Statistics* 20, 91-94.

Lindsey, C.C. (1988). Factors controlling meristic variation. In 'Fish Physiology, Vol XIB'. (Eds W.S. Hoare and D.J. Randall), Academic Press, San Diego.

Lowe, R.T. (1833). Characters of a new genus *Leirus*, and of several new species of fishes from Madeira. *Procedings of the Zoological Society of London* 1, 142-144.

Lowry, P.S., Elliott, N.G., Yearsley, G.K., and Ward, R.D. (1996). Genetic variation and phylogenetic relationships amongin seven oreo species (Teleostei, Oreosomatidae), inferred from allozyme analysis. *Fishery Bulletin US*, in press.

Lyle, J.M, Riley, S., and Kitchener, J. (1992). Oreos - an underutilised resource. *Australian Fisheries* 51 (4), 12–15.

Lyle, J.M., and Ford, W.B. (1993). 'Review of Trawl Research 1979-1987 with Summaries of Biological Information for the Major Species'. Technical Report 46, Department of Sea Fisheries, Tasmania. 169 pp.

MacDonald, C.M. (1980). 'Population Structure, Biochemical Adaptation and Systematics in Temperate Fishes of genera *Arripes* and *Chrysophrys* (Pisces: Perciformes)'. PhD thesis, Australian National University, Canberra.

Maul, G. (1948). Quatro peixes novos dos Mares de Madeira. *Boletim do Museu Municipal do Funchal* 3(6), 41-55.

McCulloch, A.R. (1914). Report on some fishes obtained by the F.I.S. "Endeavour" on the coasts of Queensland, New South Wales, Victoria, Tasmania, South and South-Western Australia. Part 2. *Biological Results of Fishing Expeditions "Endeavour"* 2 (3), 77-165.

McElroy, D., Moran, P., Bermingham, E., and Kornfield, I. (1992). REAP: an itegrated environment for the manipulation and phylogenetic analysis of restriction data. *Journal of Heredity* 83, 157–158.

Miller, R.G. (1993). 'A History and Atlas of the Fishes of the Antarctic Ocean'. Forester Institute, Nevada.

Milton, D.A., and Shaklee, J.B. (1987). Biochemical genetics and population structure of blue grenadier, *Macruronus novaezelandiae* (Hector) (Pisces: Merluccidae), from Australian waters. *Australian Journal of Marine and Freshwater Research* 38, 727-742.

Myers, G. (1960). A new zeomorph fish of the family Oreosomatidae from the coast of California, with notes on the family. Standford Ichthyological Bulletin 7, 89–98.

Nei, M. (1973). Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences USA* 70, 3321–3323.

Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89, 583–590.

Nei, M. (1987). 'Molecular Evolutionary Genetics'. Columbia University Press, New York.

Nei, M., and Tajima, F. (1981). DNA polymorphisms detectable by restriction endonuclease. *Genetics* 97, 145–163.

Ovenden, J.R., Brasher D.J., and White R.W.G. (1992). Mitochondrial DNA analysis of the red rock lobster (*Jasus edwardsii*) supports an apparent absence of population subdivision throughout Australasia. *Marine Biology* 112, 319-326.

Park, L.K., Brainard, M.A., Dightman, D.A., and Winans, G.A. (1993). Low levels of intraspecific variation in the mitochondrial DNA of chum salmon (*Oncorhnchus keta*). *Molecular Marine Biology and Biotechnology* 2, 362-370.

Paulin, C., Stewart, A., Roberts, C., and McMillan, P. (1989). 'New Zealand Fish - A Complete Guide'. National Museum of New Zealand Miscellaneous Series. No. 19.

Paxton, J.R., and Colgan, D.J. (1993). 'Biochemical Genetics and Stock Assessment of Common Gemfish and Ocean Perch'. Final Report to the Fisheries Research and Development Corporation, No. 91/35. 74 pp.

Regan, C.T. (1908). Report on the fishes collected by Mr J. Stanley Gardiner in the Indian Ocean, *Transactions of the Linnean Society of London, Zoology.* (2)12, 217–255.

Richardson, J. (1843). Contributions to the ichthyology of Australia. *Annals and Magazine of Natural History* 11, 170.

Roff , D.A., and Bentzen, P. (1989). The statistical analysis of mitochondrial DNA polymorphisms: $\chi 2$ and the problem of small samples. *Molecular Biology and Evolution* 6, 539–545.

Rogers, J.S. (1972). Measures of genetic similarity and genetic distance. *Studies in Genetics VII, University of Texas Publications* 7213, 145–153.

Ropson, I.J., Brown, D.C., and Powers, D.A. (1990). Biochemical genetics of *Fundulus heteroclitus* (L.) VI. Geographic variation in the gene frequencies of 15 loci. *Evolution* 44, 16–26.

Rosen, D.E. (1984). Zeiforms as primitive plectognath fishes. *American Museum Novitates* 2782, 1–45.

Sambrook, J., Fritsch, E.F., and Maniatis, T. (1989). 'Molecular Cloning: a Laboratory Manual (2nd ed.)'. Cold Spring Harbor Laboratory, New York, N.Y.

Seeb, L.W., Seeb., J.E., and Polvina, J.J. (1990). Genetic variation in highly exploited spiny lobster *Panulirus marginatus* populations from the Hawaiian archipelago. *Fisheries Bulletin, US*, 88, 713-718.

Shaklee, J.B., Allendorf, F.W., Morizot, D.C., and Whitt G.S. (1990). Gene nomenclature for protein-coding loci in fish. *Transactions of the American Fisheries Society* 119, 2–15.

Shcherbachev, Y.N. (1987). Preliminary list of thalassobathyal fishes of the tropical and subtropical waters of the Indian Ocean. *Journal of Ichthyology* 27, 37-46.

Shimuzu, T. (1983). Oreosomatidae. In, 'Fishes trawled off Suriname and French Guiana' (eds. T. Uyeno, K. Matsuura and E. Fujii). Japan Marine Fishery Resource Research Centre. 519pp.

Smith P.J., McKoy J.L., and Machin P.J. (1980). Genetic variation in the rock lobsters *Jasus edwardsii* and *J. novaehollandiae. New Zealand Journal of Marine and Freshwater Research* 14, 55-63.

Smith, P.J. (1986). Genetic similarity between samples of the orange roughy *Hoplostethus atlanticus* from the Tasman sea, south-west Pacific Ocean and north-east Atlantic Ocean. *Marine Biology* 91, 173–180.

Smith, P.J., and Fujio, Y. (1982). Genetic variation in marine teleosts: high variability in habitat specialists and low variability in habitat generalists. *Marine Biology* 69, 7–20.

Smith, P.J., Francis, R.I.C.C., and McVeagh, M. (1990). Loss of genetic diversity due to fishing. *Fisheries Research* 10, 309-316.

Smolenski, A.J., Ovenden, J.R., and White, R.W.G. (1993). Evidence of stock separation in southern hemisphere orange roughy (*Hoplostethus atlanticus,* Trachichthyidae) from restriction-enzyme analysis of mitochondrial DNA. *Marine Biology* 116, 219-230.

Stewart, B.D., Fenton, G.E., Smith, D.C., and Short, S.A. (1995). Validation of otolith-increment age estimates for a depwater fish species, the warty oreo *Allocyttus verrucosus*, by radiometric analysis. *Marine Biology* 123, 29-38.

Swofford, D.L. (1991). 'PAUP: Phylogenetic Analysis using Parsimony, Version 3.0s'. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois, USA.

Swofford, D.L., and Selander, R.B. (1981). BIOSYS-1: a Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *Journal of Heredity* 72, 281–283.

Tautz, D. (1989). Hypervariability of simple sequences as a general source for polymorphic DNA markers. *Nucleic Acids Research* 17, 6463-6471.

Tighe, K.A., and M.J. Keene. (1984). Zeiformes: development and relationships. In, 'Ontogeny and Systematics of Fishes' (ed. H.G. Moser) pp 393–398. Special Publication 1, American Society of Ichthyologists and Herpetologists.

Trunov, I. (1982). Zeiformes of the thalassobathyal of the southeastern Atlantic. *Bulletin of the Moscow National Society of Biological Sciences* 87, 41–53.

Ward, R.D., and Elliott, N.G. (1993). Heterozygosity and morphological variability in the orange roughy, *Hoplostethus atlanticus* (Teleostei: Trachichthyidae). *Canadian Journal of Fisheries and Aquatic Sciences,* 50, 1641-1649.

Ward, R.D., and Grewe, P.M. (1994). Appraisal of molecular genetic techniques in fisheries. *Reviews in Fish Biology and Fisheries* 4, 300-325.

Ward, R.D., Elliott, N.G., and Grewe, P.M. (1995). Allozyme and mitochondrial DNA separation of Pacific northern bluefin tuna (*Thunnus thynnus orientalis*) from southern bluefin tuna (*Thunnus maccoyii*). *Marine and Freshwater Research* 46, 921-930.

Ward, R.D., Elliott, N.G., Grewe, P.M., and Smolenski, A.J. (1994a). Allozyme and mitochondrial DNA variation in yellowfin tuna (*Thunnus albacares*) from the Pacific Ocean. *Marine Biology* 118, 531–539.

Ward, R.D., Skibinski, D.O.F., and Woodwark, M. (1992). Protein heterozygosity, protein structure and taxonomic differentiation. *Evolutionary Biology* 26, 73–159.

Ward, R.D., Woodwark, M., and Skibinski, D.O.F. (1994b). A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *Journal of Fish Biology* 44, 213–232.

Whitley, G.P. (1929). Studies in ichthyology. No. 3. *Records of the Australian Museum* 17, 101-143.

Wright, J.M., and Bentzen, P. (1994). Microsatellites: genetic markers for the future. *Reviews in Fish Biology and Fisheries* 4, 384-388.

Zehren, S.J. (1979). 'The Comparative Osteology and Phylogeny of the Beryciformes (Pisces: Teleostei)'. Evolutionary Monographs, University of Chicago.

Know Your Catch
Oreo Resources of Australia

The correct identification of the catch is crucial to research and management of fisheries. Oreos are becoming an increasingly important component of the South East Fishery catch but are proving difficult to distinguish from one another. Gordon Yearsley, of the CSIRO Division of Fisheries, presents a guide to the six species recorded from Australian waters.

(This work was partly funded by the Fisheries Research and Development Corporation.)

Oreos, oreo dories or warty dories belong to the family Oreosomatidae; they are distinguished from the closely related dories (Zeidae) by having scales on top of the head and huge eyes. Oreos are near-bottom (demersal) fishes which live in deepwater (400–1400m) over the continental slopes of most temperate, and some tropical and subtropical, regions worldwide. They feed mostly on molluscs, shrimps and fishes.

Juveniles differ markedly from the adults, so much so that the adult and juvenile oxeye oreo *(Oreosoma atlanticum)* were originally described as separate species! Most juveniles have an enlarged abdomen, sporting one or two rows of cones, protuberances or warts.

Oreos are slow growing and probably live for more than 100 years. Their maximum lengths range from 22–68 cm. The largest, the smooth oreo, can weigh up to 6.5 kg.

An oreo fishery has developed in Australia during the last 10 years. Less than 100 t per annum were retained before 1987 but the 1992 catch was over 3,000 t. Over 1,000 t were retained in 1993 and 1994. In New Zealand waters, about 19,000 t of oreos are caught anually.

Factors contributing to the increase in local catch include: reductions in orange roughy *(Hoplostethus atlanticus)* catch limits (and consequent targetting of oreos), the development of new deepwater fishing grounds, and growing market awareness.

The correct marketing names for oreos in Australia are:

- **BLACK OREO** — *Allocyttus niger and A. verrucosus,*
- **SPIKEY OREO** — *Neocyttus rhomboidalis,*
- **SMOOTH OREO** — *Pseudocyttus maculatus.*

Australian Oreos

Of the 11 oreo species known worldwide, six live in Australian waters, off the southern two-thirds of the continent and associated seamounts.

Four are fished commercially: *Allocyttus niger*, **black oreo**; *Allocyttus verrucosus*, **warty oreo**; *Neocyttus rhomboidalis*, **spikey oreo**; and *Pseudocyttus maculatus*, **smooth oreo**. The other two (*Neocyttus* sp, **rough oreo**; and *Oreosoma atlanticum*, **oxeye oreo**) are small (< 25 cm total length) and therefore discarded.

Oreos have rhomboidal or oval bodies which are deep and laterally compressed, and the head and eyes are very large. The scales of most species, although very small, have numerous sharp projections (ctenii), making the fishes rough to touch.

Some diagnostic features of Australian oreos are as follows:

Black oreo: Body rhomboidal. Combined dorsal-fin spines and rays (CD) 37–41 and combined anal-fin spines and rays (CA) 31–35. Gill-rakers on the first arch (GR) 28–36 and vertebrae 39–41. Dark grey or black; juveniles pale blue/grey with darker irregular blotches and reticulations.

Warty oreo: Body weakly rhomboidal. CD 30–39 and CA 28–32. GR 18–30 and vertebrae 36–38. Dark brown or bluish grey; juveniles paler with blue roundish blotches.

Spikey oreo: Body extremely rhomboidal. CD 38–43 and CA 32–38. GR 19–27 and vertebrae 39–41. Light or dark grey or pale brown; juveniles bluish grey.

Rough oreo: Body moderately rhomboidal. CD 36–39 and CA 30–34. GR 21–25 and vertebrae 38–39. Pale to greyish brown. The rough oreo is new to science and will be formally described by Yearsley and Last in a later publication.

Oxeye oreo: Body rhomboidal. CD 35–37 and CA 31–32. GR 27–32 and vertebrae 37–39. Pale brown; small juveniles dark grey or black.

Smooth oreo: Body oval, almost round in juveniles. CD 37–40 and CA 31–37. GR 22–31 and vertebrae 41–43. Dark greyish blue or brown (large individuals relatively pale); juveniles pale greyish blue with dark blue spots and blotches.

Below: A large oreo catch on the 'Megisti Star'. (Photo: Sean Riley, DPIF, Tasmania)

... continued on page 28

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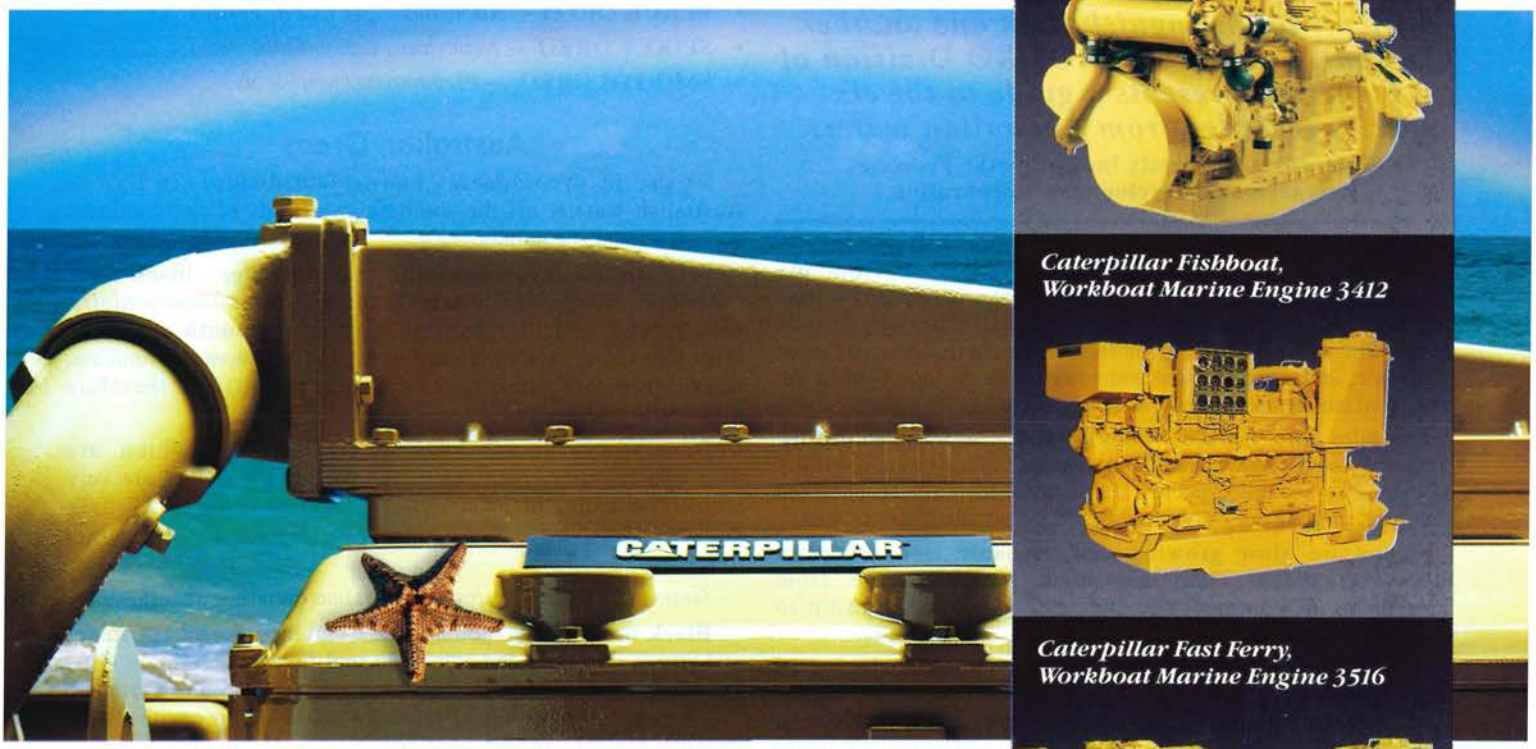

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Oreo Identification Key

Check the characteristics of your specimen against this key starting at number (1). One identifier (either (i) or (ii) should match your specimen. Follow the directions until the identification of your specimen is revealed. (Photos by Thor Carter, CSIRO Division of Fisheries.)

... *continued from page 26*

1. Does it have:

(i) The first dorsal-fin spine longer than the spine following and 1 spine and 5 soft rays in the pelvic fin? **It's the smooth oreo, *Pseudocyttus maculatus* (Figure 1, up to 68 cm total length (TL), circumglobal in southern temperate/subantarctic waters)**

(ii) The first dorsal-fin spine shorter than the spine following and 1 spine and 6 or 7 (rarely 5) soft rays in the pelvic fin? **Go to next set of identifiers (2)**

2. Does it have:

(i) A smooth body (scales on sides cycloid, deciduous) and a prominent horizontal ridge (no radiating striations) on the operculum (immediately behind eye)? **It's the oxeye oreo, *Oreosoma atlanticum* (Figure 2, up to 22 cm TL, circumglobal in southern temperate waters)**

(ii) A body rough to touch (scales on most of body ctenoid) and radiating striations (only a weak horizontal ridge) on operculum (immediately behind eye)? **Go to next set of identifiers (3)**

3. Does it have:

(i) A strongly concave predorsal profile, no plates or protuberances on the abdomen and a light grey or light brown body? **Go to next set of identifiers (4)**

(ii) An almost straight or moderately concave predorsal profile, plates or protuberances on the abdomen (occasionally absent in large specimens of *Allocyttus niger*) and a dark grey, dark brown or black body? **Go to last set of identifiers (5)**

4. Does it have:

(i) A scaled snout, 19–22 rays in the pectoral fin and a combined anal-fin spine and ray count of 32–38? **It's the spikey oreo, *Neocyttus rhomboidalis* (Figure 3, up to 48 cm TL, circumglobal in southern temperate and sub-tropical waters)**

(ii) A naked snout, 16–18 rays in the pectoral fin and a combined anal-fin spine and ray count of 30–34? **It's the rough oreo, *Neocyttus* sp (Figure 4, up to 24 cm TL, recorded from off Western Australia and Tasmania)**

5. Does it have:

(i) A double row of flat bony plates on the lower abdomen, a combined dorsal-fin spine and ray count of 33–37 and the pelvic-fin spine not reaching to the anal opening? **It's the warty oreo, *Allocyttus verrucosus* (Figure 5, up to 37 cm TL, circumglobal in southern temperate waters and further north in the Atlantic ocean)**

(ii) A single row of four low protuberances on the lower abdomen (occasionally absent or reduced to a scar in large specimens), a combined dorsal-fin spine and ray count of 37–41 and the pelvic-fin spine reaching to or beyond the anal opening? **It's the black oreo, *Allocyttus niger* (Figures 6&7, up to 49 cm TL, recorded from southern Australia and NZ).**

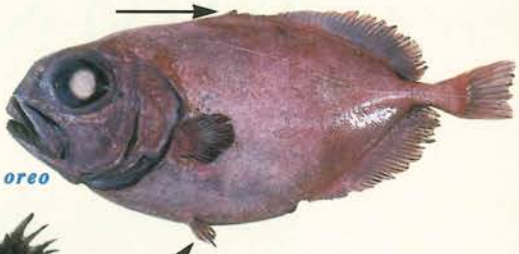

Figure 1. Smooth oreo

Figure 2. Oxeye oreo

Figure 3. Spikey oreo

Figure 4. Rough oreo

Figure 5. Warty oreo

Figure 6. Black oreo

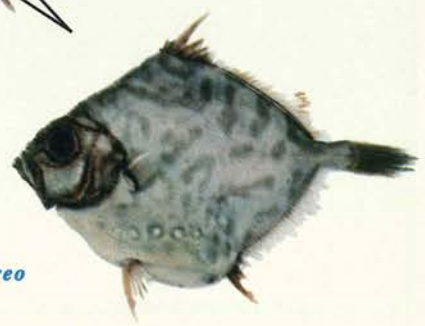

Figure 7. Juvenile black oreo

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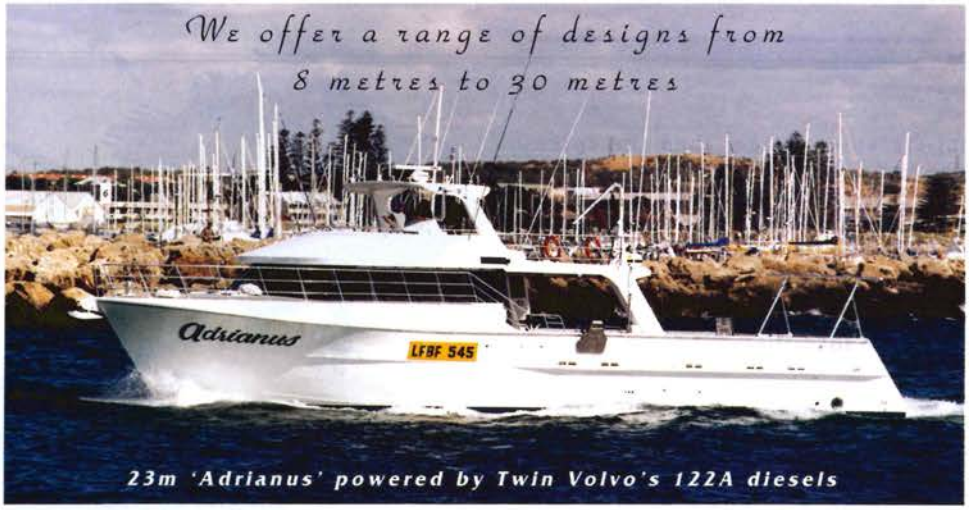

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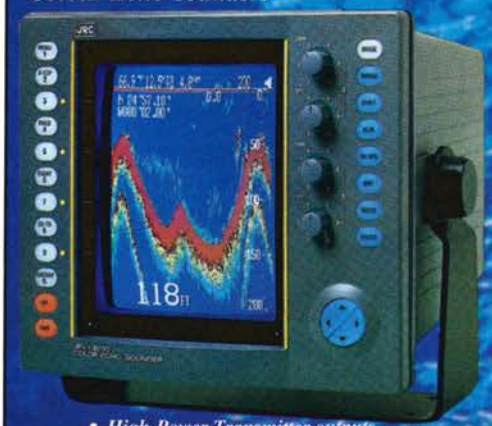

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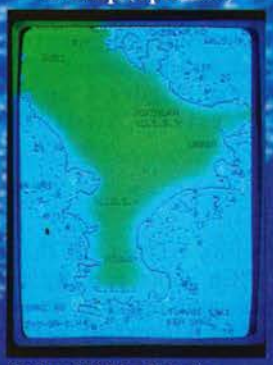
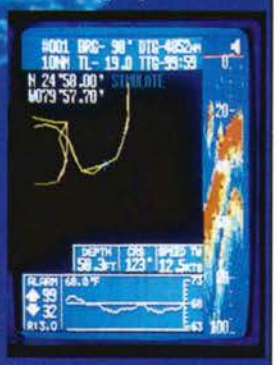


Optional C-Map Interface must have input from a GPS receiver.

Track Plotter with water temp. graph.



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C.H. SMITH MARINE	C.H. SMITH MARINE	TMQ ELECTRONICS	McCORKILLS MARINE	C.H. SMITH MARINE	C.H. SMITH MARINE	C.H. SMITH MARINE
03 417 1077	02 477 6022	07 396 7245	09 335 4800	002 34 6866	003 319044	03 417 1077

APPENDIX 2: MORPHOMETRIC AND MERISTIC DATA COLLECTED FOR TAXONOMIC COMPARISONS OF OREOS.

Table 1. Morphometric data collected for taxonomic comparisons of oreos (not *Neocyttus*). Standard length (SL) measurements are in mm; all others are expressed as a percentage of SL. Abbreviations are defined in "Materials and Methods" (section 5.3.1).

	Allocyttus folletti										
Reg.	UW22695	UW22697	UW22696	UW20831	UW22699	UW22694	UW20832	UW22698	CAS26784	CAS77127	UW22693
SL	293.9	296.5	317.0	164.0	276.1	217.1	210.4	236.1	171.5	244.1	98.0
BD	53.5	57.6	53.6	59.3	56.3	53.4	58.9	58.0	56.6	56.9	73.8
HL	35.5	36.5	33.4	40.6	34.9	38.1	38.7	37.3	38.8	36.9	36.7
HW	20.5	22.3	20.6	24.3	21.4	23.7	24.4	23.5	20.8	21.1	27.8
OD	18.0	17.5	16.2	22.0	16.6	20.9	19.8	20.1	18.0	17.2	17.7
PDL	51.2	53.9	50.5	56.1	52.3	55.4	56.3	54.4	54.6	53.7	58.6
1DSH	2.2	2.0	2.6	3.5		3.3	3.7		3.8	1.8	
2DSH	8.3	9.2	8.9	12.5		11.6	10.5		11.9	7.5	
2DSL	1.2	1.5	1.4	1.9		1.6	1.8		1.8	1.4	
VAO	18.9	20.3	16.8	20.6	21.5	13.9	16.5	19.7	18.0	18.7	62.2
LW	1.7	1.8	1.8	2.2	2.4	2.4	2.1	2.2	2.0	2.1	3.3

	Allocyttus guineensis
Reg.	UN9410001
SL	195.8
BD	57.0
HL	38.6
HW	22.4
OD	16.9
PDL	56.2
1DSH	1.5
2DSH	3.9
2DSL	1.1
VAO	25.2
LW	3.8

	Allocyttus niger													
Reg.	H2333.03	H2333.06	H2333.05	H3972.02	H2333.04	H2333.01	H3739.01	H2333.02	H2816.03	T349	H2134.01	H3167.01	T709	H1431.01
SL	272.0	227.0	227.0	281.7	236.3	265.3	209.2	255.4	223.4	218.0	193.0	195.2	202.1	198.4
HL	35.6	36.6	36.6	39.1	38.8	38.4	35.9	37.9	35.1	32.7	32.6	31.9	32.4	31.7
HW	23.3	20.8	21.1	21.9	21.1	23.0	22.4	22.5	20.0	22.1	21.2	21.1	20.2	19.6
OD	16.5	18.1	17.5	17.0	21.1	18.5	19.0	19.3	16.1	12.7	13.6	12.1	13.3	15.2
PDL	54.4	55.0	55.3	52.9	59.0	56.1	54.4	58.2	56.9	52.9	54.3	50.7	50.5	51.3
1DSH			5.0	4.5	4.5	4.4	4.0	5.7	7.3	6.0	6.9	6.0		5.5
2DSH			15.0	14.4	17.3	15.0	17.7		16.7	17.7	18.2	19.5	18.7	18.8
2DSL	2.1	2.8	2.1	2.3	2.8	2.5	2.5	2.5	2.6	2.6	3.0	2.5	2.6	2.8
VAO	17.5	19.8	16.9	17.7	17.9	15.5	17.0	16.6	18.3	28.1	24.2	28.4	29.2	25.0
LW	3.6	3.0	2.9	3.4	3.4	2.8	3.3	3.7	3.7	4.4	3.6	3.6	3.6	4.0

Table 1. continued.

	Allocyttus verrucosus													
Reg.	H3282.06	T75	H3282.01	H2626.02		H3282.02	T66	T802	H3282.03	H3282.05	H1544.01	H2977.01	T1908.04	T1567
SL	253.8	225.9	218.3	223.3	205.5	204.4	251.8	273.6	231.1	235.3	87.0	82.5	86.4	80.5
BD	53.1	63.0	63.2	60.4	61.7	68.0	57.2	57.2	56.1	66.2	75.3	66.9	69.7	73.3
HL	38.3	40.9	36.6	38.9	41.9	40.1	38.6	38.8	37.3	39.7	41.0	40.4	40.9	39.4
HW	22.6	21.8	22.5	24.2	27.4	23.4	22.5	23.9	20.8	23.6	23.4	23.0	23.8	22.7
OD	20.2	18.7	17.7	17.8	20.6	19.0	18.2	17.7	17.5	18.4	19.9	19.9	20.1	19.6
PDL	53.7	52.1	54.7	55.2	57.9	58.4	53.9	53.5	51.0	55.9	60.9	61.8	61.8	60.9
1DSH	1.5	1.9	1.7	1.0	1.9	1.2	1.5	0.9		2.1	3.6	4.6	4.9	6.8
2DSH		9.1	7.7	7.7	7.9	8.8		5.4	8.1	6.8	15.4	12.7	11.8	14.7
2DSL	0.8	1.6	1.4	1.3	1.4		1.2	1.1		1.5	2.8	2.1	2.8	2.6
VAO	19.2	23.1	23.0	21.2	21.5	21.6	19.7	19.4	19.5	22.6	32.2	29.5	26.7	33.0
LW	3.4	3.6	3.7	3.5	4.0	3.7	3.3	3.3	3.5	3.8	3.4	3.0	2.9	3.9

	Allocyttus verrucosus (cont.)			
Reg.	T1567	T1567	T1567	T1567
SL	87.0	92.6	89.0	88.0
BD	78.2	74.5	75.7	69.4
HL	42.3	39.8	42.7	39.8
HW	22.4	21.4	24.3	22.5
OD	19.9	19.4	21.9	19.3
PDL	63.2	61.0	61.2	60.2
1DSH	5.7	4.5	5.6	5.0
2DSH	15.4	11.9	15.7	15.9
2DSL	2.2	2.2	2.8	2.5
VAO	34.5	30.1	27.1	35.0
LW	2.5	3.6	3.3	3.5

	Oreosoma atlanticum													
Reg.	H1398.01	H2863.02	H1394.01	H1384.01	H3016.01	H3016.04	H884.01	H2863.01	H3016.05	H2699.01	B1650	H973.02	H3701.01	H3699.01
SL	97.1	117.8	104.9	103.4	135.0	146.0	161.9	132.8	146.9	97.1	117.8	104.9	103.4	135.0
BD	68.1	69.7	65.8	68.0	72.2	70.4	77.6	74.5	72.9	67.9	63.1	72.9	76.7	73.0
HL	36.2	36.2	36.1	36.0	37.3	38.4	32.6	35.1	39.6	38.7	39.5	40.7	37.7	32.7
HW	23.2	23.8	22.3	23.1	24.1	25.3	24.6	23.1	24.0					
OD	22.2	21.2	20.5	20.5	21.9	22.5	19.6	20.9	23.1	20.7	20.4	20.6	19.3	16.2
PDL	53.7	45.6	52.4	53.4	56.0	55.0	52.5	53.7	55.5	62.9	53.2	61.7	60.0	52.7
1DSH	5.7	5.3	4.5	5.3	5.9	5.3		4.2	5.8					

Table 1. continued.

2DSH	15.5	15.3	15.8	14.7	15.4	13.1		13.4	12.6					
2DSL		1.2	1.7	1.7	1.6	1.6	1.5	1.7	1.3					
VAO	19.7	15.4	18.8	18.7	16.2	19.0	22.0	16.8	19.1	44.0	45.2	45.3	42.8	52.5
	Oreosoma atlanticum (cont.)													
Reg.	H3262.01	A4278	H2514.01											
SL	146.0	161.9	132.8											
BD	65.4	70.2	68.6											
HL	39.6	39.7	33.7											
HW														
OD	19.6	21.9	17.9											
PDL	56.7	60.1	51.9											
1DSH														
2DSH														
2DSL														
VAO	40.7	46.4	50.6											
	Pseudocyttus maculatus													
Reg.	H3972.01	H1293.03	H2711.01	H3008.01	H3742.01	H2702.01	H1566.34	T73						
SL	393.0	366.0	341.0	210.5	219.4	176.5	159.4	171.3						
BD	46.2	47.0	44.4	55.9	59.3	61.5	64.7	54.8						
HL	37.0	32.1	31.8	37.6	37.6	36.4	36.6	38.3						
HW	21.1	16.5	17.9	19.0	20.1	17.3	18.9	19.2						
OD	16.0	14.0	13.4	17.7	16.4	16.0	17.2	18.6						
PDL	50.0	47.6	45.8	53.0	55.0	52.5	51.7	54.9						
1DSH			3.7	8.2	5.8	9.8	10.4	9.8						
2DSH			3.6	4.8	6.2	8.1	8.9	5.8						
2DSL	0.5	0.4	0.5	0.7	0.5	0.7	0.7	0.5						
VAO	26.4	23.6	21.1	24.7	24.8	26.6	26.1	22.3						

Table 2. Meristic data collected for taxonomic comparisons of oreos (not *Neocyttus*). Abbreviations are defined in "Materials and Methods" (section 5.3.1).

	Allocytus folletti												
Reg.	UW22697	UW22698	UW22696	UW20831	UW22694	UW20832	UW22699	UW22695					
DS	6	7	7	6	6	7	7	7					
DR	33	32	31	32	32?	32	32	31					
CD	39	39	38	38	38?	39	39	38					
AS	2	3	3	3	3	3	3	3					
AR	29	30	30	30	29	31	31	30					
CA	31	33	33	33	32	34	34	33					
V(L)	1,6	1,6	1,6	1,6	1,6	1,6	1,6	1,6					
P(L)	21	20	20	19	20	20	19	19					
GR(L)	4,1,20	4,21	?,19	6,20	5,20	5,19	4?,17	5,19					
TGR(L)	25	25	?	26	25	24	21?	24					
LL	92	96	90	83?	86?	88?	100	94					
Vert		39		39	39	39		39					
	Allocyttus guineensis												
Reg.	ZIL45501	ZIL45501A	ZIL45502	ZIL45503									
DS	5?	6?		6									
DR	29?			29									
CD	34?			35									
AS	3?	3		3									
AR	26?	26		25									
CA	29?	29		28									
V(L)				1,6									
P(L)				17									
GR(L)				(2),4,20									
TGR(L)				26									
LL				91									
Vert	37	37	36	37									
	Allocyttus niger												
Reg.	H2333-01	H2333-02	H2333-03	H2333-04	H2333-06	H2135-01	T703	T349	H2134-01	T709	H1431-01	H1424-02	H1378-03
DS	6	6	7	7	6	7	8	8	7	7	7	7	6
DR	33	32	32	31	32	31	31	30	32	32	30	31	32
CD	39	38	39	38	38	38	39	38	39	39	37	38	38

Table 2. continued.

AS	2	3	3	3	2	3	3	2	3	3	3	3	3
AR	30	30	30	29	30	29	30	30	30	29	30	30	29
CA	32	33	33	32	32	32	33	32	33	32	33	33	32
V(L)	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6
P(L)	19	19	19	19	19	18	21	19	20	19	19	18	19
GR(L)			(1)24(3)	28(1)	(1)26(2)					27(2)			
TGR(L)	30	30	28	29	29	31	32	30	29	29	29	31	30
LL	102	93	92	103	100	105	91+	99	97	95	100	98	108
Vert	41	39	39	39			39	40					
	Allocyttus niger (cont.)												
Reg.	H2333-05	H2821-01	H2816-03										
DS	7	7	7										
DR	32	34	30										
CD	39	41	37										
AS	3	2	3										
AR	31	31	30										
CA	34	33	33										
V(L)	1, 6	1, 6	1, 6										
P(L)	20	19	19										
GR(L)		27(2)											
TGR(L)	31	29	28										
LL	109	99	103										
Vert		40	39										
	Allocyttus verrucosus												
Reg.	H2985-03	H3035-06	H1201-05	H2036-01	T75	T58	H1566-06	T802	T657	H2626-03	H1544-01	T1567 (1)	T1567 (2)
DS	7?	6	5	5	7	7	7	6	6				
DR	30	29	30	30	28	29	30	30	30				
CD	37?	35	35	35	35	36	37	36	36				
AS	2	2	2	2	3	2	3	3	3				
AR	28	27	29	27	28	28	28	27	27				
CA	30	29	31	29	31	30	31	30	30				
V(L)	1, 6	1, 6	1, 6	1, 6	1, 6	1, 6	1, 5	1, 6	1, 6				
P(L)	18	19	18	19	18	19	18	17	18				

Table 2. continued.

GR(L)					21(3)	(1)19(3)	(1)22(2)	20 (4)					
TGR(L)	24	22	24	22	24	23	25	24	20				
LL	94	85	~89	87	92	85	90	96	88				
Vert							37		37	36	37	38	37
	Allocyttus verrucosus (cont.)												
Reg.	T1567 (3)	T66	H1566-05										
DS													
DR													
CD													
AS													
AR													
CA													
V(L)													
P(L)													
GR(L)													
TGR(L)													
LL													
Vert	36	37	37										
	Oreosoma atlanticum												
Reg.	H2699-01	H2863-01	H3016-01	H884-01	H3016-04	H3016-05	H2514-01						
DS	4?	7?	6	8	6	6	6						
DR	32	28	30	28	31	29	29						
CD	36?	35?	36	36	37	35	35						
AS	2?	4	3	?	3	3	1?						
AR	29	28	28	27	29	28	25?						
CA	31?	32	31	?	32	31	26?						
V(L)	1,6?	1?,5	1,6	1,6	1,6	1,7	1,5?						
P(L)	21	20	20	20	20	20	22						
TGR(L)		27	31	28	30	32							
LL		94	102	94	96?	95	96						
Vert	37	37	38	39	38	38	37						

Table 2. continued.

	Pseudocyttus maculatus												
Reg.	H1293.03	H3008-01	H3008-14	H2702-01	H1566-34								
DS	5	6	6	5	6								
DR	34	34	33	35	34								
CD	39	40	39	40	40								
AS	3	3	2	3	3								
AR	32	31	32	32	32								
CA	35	34	34	35	35								
V(L)	1,5	1,5	1,5	1,5	1,5								
P(L)	20	20	20	21	21								
TGR(L)	26	25	26	26	26								
LL	103	102?	93?	114?	110								
Vert	43	42	41	42	42								

Table 3. Proportional measurements and meristic values for the holotype and one other specimen of *Neocyttus acanthorhynchus*. Total and standard lengths are in millimetres; unless otherwise stated, all other measurements are expressed as a percentage of standard length. "D" signifies damage that prevented a reliable measurement.

	Holotype BMNH1908.3.23.122	**MNHN1979 0419**
Total length	115	181
Standard length	99	152
Body depth	60.8	62.9
Head length	34.9	30.9
Head depth	25.3	23.9
Head width	20.4	19.2
Snout length	7.7	6.8
Upper jaw length	12.7	11.0
Lower jaw length	17.3	16.0
Postorbital head length	11.4	10.6
Lachrymal width	3.2	3.6
Orbit diameter	17.5	15.5
Interorbital width	13.5	11.8
Caudal peduncle depth	6.3	6.4
Caudal peduncle length	13.5	13.9
Predorsal length	50.9	47.8
Preanal length	57.1	60.9
Dorsal-fin base length	53.0	54.9
Anal-fin base length	43.9	45.9
First dorsal-fin spine height (1DSH)	3.5	3.1
Second dorsal-fin spine height (2DSH)	15.5	D
Second dorsal-fin spine length	2.0	1.5
Dorsal-fin ray length	12.6	13.6
Dorsal-fin origin to lateral line	18.7	18.4
First anal-fin spine height	13.6	D
First anal-fin spine length	1.9	1.6
Anal-fin ray length	12.8	14.3
Pectoral-fin length	13.2	14.4
Pelvic-fin spine length	18.8	
Pelvic-fin length	20.6	19.1
Pelvic-fin insertion to anal-fin origin	11.2	16.1
Thoracic-ridge length	25.5	25.7
Pectoral-fin insertion to pelvic-fin origin (PV)	15.6	18.0
Pectoral-fin insertion to anal-fin origin (PA)	17.1	20.1
PV/PA	91.1	89.8
Orbit diameter/head length	50.0	50.0
2DSH/1DSH	4.4	D
Dorsal-fin spines	7	9
Dorsal-fin rays	31	30
Dorsal-fin spines and rays	38	39
Anal-fin spines	3	3
Anal-fin rays	29	29
Anal-fin spines and rays	32	32
Ventral-fin spines	1	1
Ventral-fin rays	6	5
Pectoral-fin rays	17	17
Gill rakers	4+17	5+17
Total gill rakers	21	22
Lateral line scales	65	75
Trunk vertebrae	10	10
Tail vertebrae	27	27
Total vertebrae	37	37

Table 4. Proportional measurements and meristic values for the holotype and four other CSIRO specimens (H3583.01, H3583.02, H3583.03 and H3583.04) of *Neocyttus helgae*. Total and standard lengths are in millimetres; unless otherwise stated, all other measurements are expressed as a percentage of standard length. "D" signifies damage that prevented a reliable measurement.

	Holotype	Other specimens			
	BMNH1910.9.17.1	n	min	max	mean	SD
Total length	235	2	282	311	296.5	20.51
Standard length	193	4	143	262	200.0	60.25
Body depth	75.9	4	69.0	83.4	77.3	6.18
Head length	33.4	4	30.7	34.3	32.4	1.48
Head depth	23.2	4	22.7	25.3	23.9	1.21
Head width	18.3	4	16.9	18.8	18.1	0.85
Snout length	9.2	4	7.8	8.7	8.3	0.37
Upper jaw length	12.0	4	11.0	11.9	11.3	0.42
Lower jaw length	16.2	4	15.3	18.0	16.7	1.12
Postorbital head length	11.8	4	10.6	12.5	11.3	0.82
Lachrymal width	4.5	4	3.2	5.3	4.3	0.87
Orbit diameter	13.9	4	12.0	15.7	13.8	1.63
Interorbital width	11.5	4	11.1	12.2	11.6	0.48
Caudal peduncle depth	7.4	4	6.7	8.0	7.4	0.54
Caudal peduncle length	15.3	4	14.2	16.4	15.4	0.92
Predorsal length	51.3	4	45.4	55.4	51.4	4.44
Preanal length	62.7	4	59.9	63.9	62.4	1.74
Dorsal-fin base length	59.8	4	57.8	63.1	60.7	2.22
Anal-fin base length	48.7	4	47.4	53.2	50.6	2.92
First dorsal-fin spine height (1DSH)	5.1	4	2.0	4.5	3.1	1.04
Second dorsal-fin spine height (2DSH)	15.2	2	12.0	14.5	13.3	1.77
Second dorsal-fin spine length	2.2	4	1.9	2.8	2.3	0.44
Dorsal-fin ray length	16.2	2	14.6	14.7	14.7	0.07
Dorsal-fin origin to lateral line	21.0	4	16.4	23.4	20.0	2.87
First anal-fin spine height	14.2	2	8.8	11.4	10.1	1.84
First anal-fin spine length	2.7	4	1.6	2.4	2.1	0.35
Anal-fin ray length	16.4	1	15.1	15.1	15.1	
Pectoral-fin length	15.6	4	13.4	15.7	14.8	1.05
Pelvic-fin spine length	13.8	0	D	D		
Pelvic-fin length	17.3	4	14.1	19.1	16.7	2.62
Pelvic-fin insertion to anal-fin origin	14.4	4	15.2	16.8	16.3	0.75
Thoracic-ridge length	28.2	4	26.7	29.8	28.0	1.40
Pectoral-fin insertion to pelvic-fin origin (PV)	19.2	4	20.0	22.0	21.0	0.84
Pectoral-fin insertion to anal-fin origin (PA)	28.9	4	28.7	33.0	30.6	1.78
PV/PA	66.6	4	66.2	72.4	68.8	2.88
Orbit diameter/head length	41.8	4	38.9	45.8	42.5	3.30
2DSH/1DSH	3.0	2	4.3	4.5	4.4	0.14
Dorsal-fin spines	7	4	6	8	7.3	0.96
Dorsal-fin rays	33	4	30	33	31.5	1.29
Dorsal-fin spines and rays	40	4	38	40	38.8	0.96
Anal-fin spines	4	4	3	4	3.8	0.50
Anal-fin rays	29	4	29	30	29.8	0.50
Anal-fin spines and rays	33	4	33	34	33.5	0.58
Ventral-fin spines	1	4	1	1	1.0	0.00
Ventral-fin rays	6	4	5	6	5.8	0.50
Pectoral-fin rays	19	4	17	19	18.0	0.82
Gill rakers	5+17	4	5+16	5+18	5+17	–+0.82
Total gill rakers	22	4	21	23	22.0	0.82
Lateral line scales	79	4	76	90	81.3	6.70
Trunk vertebrae	11	4	11	11	11.0	0.00
Tail vertebrae	29	4	28	29	28.8	0.50
Total vertebrae	40	4	39	40	39.8	0.50

Table 5. Proportional measurements and meristic values for two paratypes and 6 other small CSIRO specimens (H3007.08, H3007.12, H3035.07, T68, T71, T1581.01) and 10 other large CSIRO specimens (H269.01, H593.01, H1566.07, H3282.09, H3282.10, H3502.01, H3592.03, H3741.01, T704, T1848.01) of *Neocyttus rhomboidalis*. Total and standard lengths are in millimetres; unless otherwise stated, all other measurements are expressed as a percentage of standard length. "D" signifies damage that prevented a reliable measurement; not all specimens were radiographed to count vertebrae.

	Paratype	Paratype	specimens <116 mm SL					specimens >177 mm SL				
	SAM11973	BMNH1904.5.28.14	n	min	max	mean	SD	n	min	max	mean	SD
Total length	114	123	6	101	138	121.0	12.28	8	263	393	333.9	45.18
Standard length	98	103	6	85	115	100.2	10.05	10	178	333	267.9	46.73
Body depth	78.1	71.9	6	72.8	79.8	76.3	2.57	10	61.9	75.0	69.5	3.86
Head length	39.6	40.8	6	37.0	41.6	39.3	1.74	10	33.8	37.8	35.8	1.15
Head depth	28.6	29.7	6	27.6	29.8	28.4	0.83	10	26.4	29.9	27.6	1.14
Head width	21.9	23.3	6	21.1	23.5	22.4	0.96	10	20.4	23.2	21.7	0.74
Snout length (direct)	9.1	8.5	6	7.7	10.1	8.6	0.89	10	7.7	8.8	8.3	0.39
Upper jaw length	13.3	14.6	6	12.8	15.8	14.5	1.02	10	14.0	16.3	15.6	0.68
Lower jaw length	18.7	20.1	6	18.0	20.4	19.2	0.79	10	17.9	20.6	19.3	0.71
Postorbital head length	11.4	12.5	6	10.7	12.4	11.5	0.59	10	11.5	13.7	12.4	0.75
Lachrymal width	2.1	2.0	6	1.9	2.7	2.4	0.30	10	2.2	3.6	2.9	0.41
Orbit diameter	21.4	22.3	6	19.9	23.4	21.5	1.37	10	16.3	19.0	17.4	0.83
Interorbital width	15.7	14.7	6	14.6	17.1	15.8	0.83	10	12.8	14.8	13.7	0.64
Caudal peduncle depth	5.2	6.4	6	6.3	7.3	6.8	0.41	10	5.9	7.5	6.6	0.42
Caudal peduncle length	8.9	13.1	6	8.6	12.4	10.3	1.34	10	9.7	12.1	11.0	0.62
Predorsal length	60.2	59.7	6	56.0	60.4	58.7	1.49	10	49.7	57.9	54.2	2.10
Preanal length	70.0	67.0	6	64.5	74.4	69.5	3.17	10	61.9	67.4	65.0	1.47
Dorsal-fin base length	57.1	52.5	6	54.5	60.0	55.8	2.07	10	53.7	59.0	56.2	1.97
Anal-fin base length	46.9	45.6	6	45.1	50.4	46.4	2.04	10	42.5	49.2	45.6	2.10
First dorsal-fin spine height (1DSH)	6.6	5.0	6	5.9	7.2	6.4	0.56	9	2.9	5.0	3.7	0.75
Second dorsal-fin spine height (2DSH)	19.8	17.5	6	18.7	25.8	21.4	2.58	6	14.2	17.2	15.8	1.08
Second dorsal-fin spine length	3.2	2.9	6	2.9	3.6	3.2	0.27	10	1.9	2.8	2.3	0.31
Dorsal-fin ray length	16.7	14.9	6	11.8	18.9	15.3	2.31	9	13.3	15.4	14.2	0.70
Dorsal-fin origin to lateral line	21.5	21.1	6	18.9	21.4	20.4	0.88	10	15.4	20.2	17.9	1.55
First anal-fin spine height	D	14.4	5	12.4	21.4	15.7	3.53	5	10.8	15.7	14.0	1.95
First anal-fin spine length	D	2.0	6	2.3	3.5	2.8	0.49	9	1.7	2.8	2.3	0.30

Table 5. continued.

	Paratype	Paratype	specimens <116 mm SL					specimens >177 mm SL				
	SAM11973	BMNH1904.5.28.14	n	min	max	mean	SD	n	min	max	mean	SD
Anal-fin ray length	17.6	14.5	5	15.4	17.6	16.3	0.92	8	13.3	15.9	14.4	1.03
Pectoral-fin length	16.8	13.3	6	12.3	17.8	15.2	1.86	10	11.1	15.5	14.0	1.19
Pelvic-fin spine length	21.8	18.1	6	16.4	24.1	19.9	2.68	9	12.9	17.7	15.4	1.81
Pelvic-fin length	23.6	21.7	6	18.6	24.2	21.5	1.95	10	15.2	18.9	17.4	1.24
Pelvic-fin insertion to anal-fin origin	17.1	16.7	6	15.8	21.0	17.7	1.99	10	13.5	18.7	16.5	1.55
Thoracic-ridge length	26.5	25.7	6	25.8	28.5	27.4	1.11	10	26.8	30.8	28.3	1.11
Pectoral-fin insertion to pelvic-fin origin (PV)	21.5	21.1	6	17.9	25.2	22.3	2.76	10	19.1	22.1	20.7	1.01
Pectoral-fin insertion to anal-fin origin (PA)	26.4	22.8	6	21.7	30.3	26.5	3.32	10	20.6	27.2	24.7	1.79
PV/PA	81.5	92.3	6	76.5	90.7	84.5	4.93	10	73.6	93.0	84.1	6.19
Orbit diameter/head length	54.1	54.8	6	51.3	58.0	54.6	2.44	10	45.4	51.4	48.7	1.56
2DSH/1DSH	3.0	3.5	6	2.8	4.3	3.3	0.56	6	3.2	4.8	4.2	0.61
								non-paratypes combined				
Dorsal-fin spines	8	7						16	7	8	7.3	0.45
Dorsal-fin rays	33	32						16	31	34	32.4	0.89
Dorsal-fin spines and rays	41	39						16	39	41	39.6	0.62
Anal-fin spines	3	4						16	3	4	3.9	0.34
Anal-fin rays	31	29						16	29	32	30.4	0.73
Anal-fin spines and rays	34	33						16	33	36	34.3	0.87
Ventral-fin spines	1	1						16	1	1	1.0	0.00
Ventral-fin rays	6	5						16	5	6	5.9	0.34
Pectoral-fin rays	21	21						15	19	21	20.5	0.64
Gill rakers	5+18	5+18						15	4+15	6+21	5+17.6	0.38+1.40
Total gill rakers	23	23						15	20	26	22.6	1.45
Lateral line scales	96	100						15	88	109	100.5	6.06
Trunk vertebrae	11	11						8	11	12	11.4	0.52
Tail vertebrae	28	29						8	27	28	27.6	0.52
Total vertebrae	39	40						8	38	40	39.0	0.53

Table 6. Proportional measurements and meristic values for 16 CSIRO specimens of *Neocyttus* sp. A. Total and standard lengths are in millimetres; unless otherwise stated, all other measurements are expressed as a percentage of standard length. "D" signifies damage that prevented a reliable measurement.

	H2865.01	H2864.01	H2864.03	H2864.04	H2864.05	H2864.06	H2864.07	H2864.08	H2864.09
Total length	181	182	190	177	216	183	203	200	189
Standard length	148	153	155	144	180	152	164	169	158
Body depth	74.2	64.7	67.7	69.6	66.7	68.8	64.9	63.6	65.6
Head length	33.8	35.4	37.3	35.7	31.9	36.5	35.5	35.4	34.4
Head depth	24.9	24.5	25.7	26.7	23.3	25.9	26.3	22.7	25.1
Head width	18.7	21.5	21.5	20.8	18.7	20.5	21.9	21.6	19.6
Snout length	8.9	9.2	9.2	8.8	7.8	9.3	8.7	9.2	8.4
Upper jaw length	12.8	13.4	14.0	13.4	11.8	13.4	13.1	12.1	12.1
Lower jaw length	17.2	17.0	18.1	18.6	16.7	18.4	17.4	16.6	16.9
Postorbital head length	11.7	11.4	12.5	11.7	11.3	12.0	12.7	12.1	11.3
Lachrymal width	4.2	4.8	4.5	5.0	4.4	4.3	5.1	4.8	4.2
Orbit diameter	15.6	17.6	18.5	16.9	15.0	17.4	16.5	15.6	17.0
Interorbital width	13.2	14.7	14.3	15.6	12.1	14.9	14.0	14.9	12.2
Caudal peduncle depth	6.8	6.2	6.6	6.6	6.4	6.3	6.4	6.3	6.1
Caudal peduncle length	14.5	13.8	14.1	15.2	11.7	13.6	15.3	13.8	16.6
Predorsal length	50.6	53.6	52.1	51.3	53.8	52.8	49.9	50.2	53.0
Preanal length	61.1	58.8	59.7	59.4	63.1	63.6	59.4	60.7	62.5
Dorsal-fin base length	58.4	55.0	56.5	56.7	52.8	52.1	55.7	53.1	53.1
Anal-fin base length	47.3	45.4	49.7	46.5	45.8	46.2	42.7	42.1	41.8
First dorsal-fin spine height (1DSH)	3.0	2.8	4.3	3.5	2.3	3.0	4.1	3.1	D
Second dorsal-fin spine height (2DSH)	16.8	13.5	14.8	17.1	D	13.8	D	D	D
Second dorsal-fin spine length	2.2	2.0	2.0	2.2	2.4	1.6	2.1	1.7	1.8
Dorsal-fin ray length	15.7	15.0	17.5	16.0	15.7	17.1	16.5	15.4	15.6
Dorsal-fin origin to lateral line	20.7	19.0	17.2	18.9	17.8	17.2	16.7	13.1	17.0
First anal-fin spine height	14.9	10.2	11.6	D	10.5	D	9.5	D	10.6
First anal-fin spine length	2.0	1.8	2.3	D	2.4	1.7	1.6	D	1.5
Anal-fin ray length	15.7	15.2	18.2	17.5	15.6	17.2	16.8	16.0	15.8
Pectoral-fin length	13.8	15.4	16.5	16.9	14.2	16.0	14.6	14.5	12.7
Pelvic-fin spine length	18.2	15.6	15.3	18.3	15.2	15.5	15.6	14.4	13.9
Pelvic-fin length	20.1	18.7	19.4	20.5	18.1	20.0	18.8	17.0	17.6
Pelvic-fin insertion to anal-fin origin	15.7	13.3	11.2	16.3	17.7	16.5	14.5	15.7	15.8

Table 6. continued.

	H2865.01	H2864.01	H2864.03	H2864.04	H2864.05	H2864.06	H2864.07	H2864.08	H2864.09
Thoracic-ridge length	28.4	25.6	26.3	26.0	26.4	26.1	24.6	25.4	27.4
Pectoral-fin insertion to pelvic-fin origin (PV)	18.6	14.2	16.2	16.9	16.7	18.6	18.2	16.6	19.0
Pectoral-fin insertion to anal-fin origin (PA)	26.4	20.9	23.9	22.5	24.2	24.5	23.4	23.1	25.7
PV/PA	70.5	67.8	67.8	75.3	69.0	76.1	77.9	71.6	73.9
Orbit diameter/head length	46.2	49.9	49.5	47.3	47.0	47.6	46.4	44.1	49.3
2DSH/1DSH	5.5	4.8	3.4	4.9	D	4.7	D	D	D
Dorsal-fin spines	8	8	7	7	7	7	7	7	7
Dorsal-fin rays	29	31	30	30	31	29	30	31	30
Dorsal-fin spines and rays	37	39	37	37	38	36	37	38	37
Anal-fin spines	4	4	4	4	3	4	4	4	4
Anal-fin rays	27	29	30	28	28	28	27	27	27
Anal-fin spines and rays	31	33	34	32	31	32	31	31	31
Ventral-fin spines	1	1	1	1	1	1	1	1	1
Ventral-fin rays	6	7	6	5	6	6	6	6	6
Pectoral-fin rays	18	18	16	17	16	17	17	17	12D
Gill rakers	6+18	4+18	6+16	4+(1)16	5+19	5+18	5+(1)16	5+20	5+17
Total gill rakers	24	22	22	21	24	23	22	25	22
Lateral line scales	73	73	80	72	78	79	79	75	88
Trunk vertebrae	10	10	10	11	10	10	10	10	10
Tail vertebrae	28	29	27	26	27	27	28	28	28
Total vertebrae	38	39	37	37	37	37	38	38	38

Table 6. continued.

H2864.10	H2864.11	H2864.12	H2864.13	H2865.02	H3294.03	H3593.01	n	min	max	mean	SD
179	173	150	143	210	197	238	16	143	238	188	23.42
147	141	124	115	172	163	201	16	115	201	155	20.63
67.2	63.9	77.1	63.3	66.2	76.2	74.3	16	63.3	77.1	68.4	4.62
34.7	34.3	38.4	37.1	36.0	35.7	33.4	16	31.9	38.4	35.3	1.61
24.7	24.5	25.5	26.1	24.1	25.8	24.8	16	22.7	26.7	25.0	1.08
20.3	19.5	19.0	19.6	19.5	19.1	17.7	16	17.7	21.9	20.0	1.23
8.2	8.4	9.2	9.0	8.5	8.2	8.1	16	7.8	9.3	8.7	0.48
12.7	12.7	12.7	14.0	13.0	14.4	13.3	16	11.8	14.4	13.1	0.72
17.3	18.2	18.7	19.8	17.2	17.7	16.9	16	16.6	19.8	17.7	0.90
12.5	12.4	12.9	11.9	12.6	13.4	12.5	16	11.3	13.4	12.2	0.62
3.7	4.8	4.8	4.0	4.4	4.8	4.4	16	3.7	5.1	4.5	0.38
16.0	15.0	18.1	17.2	17.0	15.7	14.0	16	14.0	18.5	16.4	1.24
12.3	12.8	15.6	14.2	10.8	11.1	13.1	16	10.8	15.6	13.5	1.51
6.6	6.0	6.8	6.7	6.9	7.4	6.5	16	6.0	7.4	6.5	0.34
18.0	16.2	14.2	13.3	16.3	15.1	13.6	16	11.7	18.0	14.7	1.55
51.1	50.7	56.9	51.0	52.0	53.7	52.4	16	49.9	56.9	52.2	1.77
60.7	60.8	61.5	63.7	61.0	63.5	64.9	16	58.8	64.9	61.5	1.83
54.4	53.5	57.3	52.2	52.1	58.7	57.4	16	52.1	58.7	54.9	2.33
45.7	44.2	50.5	43.9	42.5	48.4	44.3	16	41.8	50.5	45.4	2.63
3.4	4.4	3.8	4.0	3.2	4.4	3.1	15	2.3	4.4	3.5	0.65
14.8	15.7	16.0	14.8	D	17.3	D	10	13.5	17.3	15.5	1.35
2.0	1.7	2.5	2.3	1.9	2.4	2.4	16	1.6	2.5	2.1	0.28
14.3	16.2	17.2	15.7	18.6	16.4	12.3	16	12.3	18.6	16.0	1.43
17.2	17.4	21.6	15.9	15.6	20.4	20.3	16	13.1	21.6	17.9	2.19
11.6	12.8	D	D	13.1	14.1	9.0	11	9.0	14.9	11.6	1.91
2.0	D	2.0	D	1.5	2.4	2.2	12	1.5	2.4	2.0	0.33
15.4	17.4	16.8	17.0	17.1	16.3	11.8	16	11.8	18.2	16.2	1.45
15.3	15.2	14.4	15.9	15.6	17.1	15.5	16	12.7	17.1	15.2	1.16
14.5	17.6	D	18.1	D	14.4	13.6	14	13.6	18.3	15.7	1.65
18.0	21.4	20.9	22.0	17.0	20.5	16.4	16	16.4	22.0	19.2	1.69
16.0	16.9	16.2	16.0	13.1	21.6	17.5	16	11.2	21.6	15.9	2.29
25.0	24.0	25.7	25.9	26.4	27.3	28.2	16	24.0	28.4	26.2	1.20
16.3	16.2	17.0	15.2	20.3	18.0	19.2	16	14.2	20.3	17.3	1.61
22.6	22.2	24.8	20.0	23.7	25.0	28.4	16	20.0	28.4	23.8	2.05
72.0	73.2	68.5	76.1	85.8	72.1	67.5	16	67.5	85.8	72.8	4.77
46.1	43.7	47.3	46.4	47.1	44.0	41.9	16	41.9	49.9	46.5	2.20

Table 6. continued.

H2864.10	H2864.11	H2864.12	H2864.13	H2865.02	H3294.03	H3593.01	n	min	max	mean	SD
4.4	3.6	4.2	3.7	D	3.9	D	10	3.4	5.5	4.3	0.68
7	7	7	7	8	7	8	16	7	8	7.3	0.45
29	30	29	29	29	30	30	16	29	31	29.8	0.75
36	37	36	36	37	37	38	16	36	39	37.1	0.85
4	4	4	4	3	3	4	16	3	4	3.8	0.40
27	26	27	27	28	28	28	16	26	30	27.6	0.96
31	30	31	31	31	31	32	16	30	34	31.4	0.96
1	1	1	1	1	1	1	16	1	1	1.0	0.00
6	6	5	6	6	6	6	16	5	7	5.9	0.44
17	18	16	17	16	17	16	15	16	18	16.9	0.74
5+(1)17	6+(1)18	4+(1)18	4+19	5+(1)17	5+(1)19	5+19	16	4+16	6+20	4.94+18.25	0.68+1.13
23	25	23	23	23	25	24	16	21	25	23.2	1.22
82	70	81	76	81	84	84	16	70	88	78.4	4.98
10	10	10	10	10	10	10	16	10	11	10.1	0.25
27	28	27	27	28	27	27	16	26	29	27.4	0.73
37	38	37	37	38	37	37	16	37	39	37.5	0.63

Table 7. Proportional measurements for one IOAN specimen of *Neocyttus* sp. B. Total and standard lengths are in millimetres; unless otherwise stated, all other measurements are expressed as a percentage of standard length. "D" signifies damage that prevented a reliable measurement.

	P15776
Total length	163
Standard length	132
Body depth	69.6
Head length	35.5
Head depth	24.7
Head width	22
Snout length	8.9
Upper jaw length	11.4
Lower jaw length	17.7
Postorbital head length	11.5
Lachrymal width	5
Orbit diameter	16.7
Interorbital width	13.6
Caudal peduncle depth	6.7
Caudal peduncle length	14.4
Predorsal length	50.3
Preanal length	66.4
Dorsal-fin base length	55.3
Anal-fin base length	44.4
First dorsal-fin spine height (1DSH)	4.5
Second dorsal-fin spine height (2DSH)	15.8
Second dorsal-fin spine length	2.6
Dorsal-fin ray length	14.5
Dorsal-fin origin to lateral line	19.7
First anal-fin spine height	D
First anal-fin spine length	3
Anal-fin ray length	15.1
Pectoral-fin length	14.9
Pelvic-fin spine length	18.1
Pelvic-fin length	20
Pelvic-fin insertion to anal-fin origin	14.8
Thoracic-ridge length	23.6
Pectoral-fin insertion to pelvic-fin origin (PV)	17.7
Pectoral-fin insertion to anal-fin origin (PA)	21.8
PV/PA	81.3
Orbit diameter/head length	46.9
2DSH/1DSH	3.5

APPENDIX 3: MITOCHONDRIAL DNA FRAGMENT SIZES

Estimated sizes of mitochondrial DNA fragments following digestion with the specified restriction enzymes. Numbers in italics are small fragments that are assumed to be present but were not apparent from the autoradiographs. - = fragment not detected.

***Afl* II**

A	B	C
12100	-	-
-	8440	-
-	-	6880
-	-	5240
4300	4300	4300
-	3650	-
16400	16390	16420

***Apa* I**

A	B	C	D	E	F	G	H	J	K	L	M	N	O
-	-	-	-	-	-	-	-	-	8790	-	8790	-	8790
-	-	-	-	-	-	-	-	-	-	8090	-	-	-
7640	-	7640	-	7640	-	-	-	-	-	-	-	-	7640
7380	7380	-	7380	-	-	-	7380	7380	-	-	7380	7380	-
-	-	-	7380	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	7240	-	-	-
-	6270	-	-	-	-	6270	-	-	-	-	-	-	-
-	-	5880	-	-	5880	-	-	-	5880	-	-	5880	-
-	-	-	-	-	-	-	5380	-	-	-	-	-	-
-	-	-	-	5280	5280	5280	-	5280	-	-	-	-	-
-	-	-	-	-	-	-		-	-	-	-	-	-
-	-	-	-	-	-	-	3750	-	-	-	-	-	-
-	-	-	-	-	2370	-	-	2370	-	-	-	-	-
-	-	-	-	2330	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	2020	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	1900	-
-	-	1780	-	-	1780	-	-	-	1780	1780	-	-	-
-	1620	-	-	-	-	1620	-	-	-	-	-	-	-
-	1380	1380	1380	1380	1380	1380	-	1380	-	1380	-	1380	-
-	-	-	*300*	-	-	-	-	-	-	-	-	-	-
16400	16650	16680	16440	16630	16690	16570	16510	16410	16450	17110	16170	16540	16430

***Apa* II**

A	B
-	15460
9890	-
5570	-
15460	15460

***Ava* I**

A	B	C	D	E	G
9230	-	-	9230	-	-
-	8400	-	-	-	8400
-	-	-	-	-	-
-	-	6545	-	-	-
-	-	-	-	5230	-
-	-	-	-	3790	-
3600	3600	3600	-	3600	3600
-	-	-	-	-	3450
-	-	2680	-	-	-
-	-	-	2340	-	-
2050	2050	2050	2050	2050	-
1625	1625	1625	1625	1625	-
-	-	-	1470	-	-
-	800	-	-	-	*800*
16505	16475	16500	16715	16295	16250

***Ban* I**

A	B
5050	5050
4640	-
3340	3340
-	2320
-	2320
1370	1370
1000	1000
870	870
670	*670*
16940	16940

***Bgl* I**

A	B	C	D
-	9570	-	-
6920	-	6920	-
-	-	-	6580
5110	5110	-	5110
-	-	3910	-
3160	-	3160	3160
-	-	2580	-
1510	1510	-	1510
-	-	-	*340*
16700	16190	16570	16700

***BstE* II**

A	B	C	D	E	F
-	16100	-	-	-	-
-	-	14160	-	-	-
-	-	-	-	-	12400
-	-	-	9990	-	-
8900	-	-	-	8900	-
7200	-	-	-	-	-
-	-	-	-	5170	-
-	-	-	2500	-	2500
-	-	1940	1940	1940	-
-	-	-	1670	-	1670
16100	16100	16100	16100	16010	16570

***Dra* I**

A	B	D	C
7090	7090	7090	7090
-	4210	-	-
-	-	-	3600
3460	-	3460	-
1740	1740	1740	1740
-	-	1490	1490
-	-	-	-
1200	1200	1200	1200
1190	1190	-	-
-	-	-	-
1110	1110	1110	1110
750	-	750	-
-	-	-	*564*
300	*300*	-	-
16840	16840	16840	16794

***Eco* RI**

A	B	C	D	E	F
-	-	-	-	16587	-
-	-	-	-	-	12937
-	-	-	11887	-	-
8340	8340	8340	-	-	-
8340	-	-	-	-	-
-	-	4700	4700	-	-
-	4400	-	-	-	-
-	3650	3650	-	-	3650
-	*300*	-	-	-	-
16680	16690	16690	16587	16587	16587

***Eco* RV**

A	B	C
13190	13190	-
-	-	8480
-	-	3870
-	3430	3430
1740	-	1740
1740	-	-
16670	16620	17520

***Hind* III**

A	B	C	D	E	F	G
10580	-	-	10580	-	-	-
-	-	-	-	8680	-	8680
-	-	8560	-	-	-	-
-	6300	-	-	-	6300	-
-	4280	4280	-	-	4280	-
-	-	-	4200	4200	4200	-
2900	2900	2900	-	-	-	2900
2260	2260	-	2260	2260	2260	2260
-	-	-	-	1890	-	1890
1300	1300	1300	-	-	-	1300
-	-	-	-	-	-	-
17040	17040	17040	17040	17030	17040	17030

***Kpn* I**

A	C
16400	-
-	10430
-	6860
16400	17290

***Pst* I**

A	B	C
-	17300	-
15060	-	-
-	-	9920
-	-	5140
2565	-	2565
17625	17300	17625

***Pvu* II**

A	B	C
7870	7870	-
-	-	5560
-	4780	4780
4470	-	-
2520	2520	2520
-	-	2360
1390	1390	1390
300	-	-
16550	16560	16610

***Sma* I**

A	B
14900	-
-	11200
-	3700
1600	1600
16500	16500

***Sty* I**

A	B	C	D
-	-	10800	-
-	-	-	5070
3650	3650	-	-
2260	2260	-	2260
-	2080	-	-
1920	-	-	1920
1600	1600	-	-
1430	1430	-	-
-	-	-	1190
800	800	-	-
560	560	-	*560*
480	480	-	-
12700	12860	10800	11000

This enzyme gives many small fragments which could not be seen, hence the apparently reduced mtDNA size.

***Xba* I**

A	B
10860	-
-	7570
5030	5030
-	3390
15890	15990