

Spatial and temporal distribution of three wrasse species
(Pisces: Labridae) in Masfjord, western Norway: habitat
association and effects of environmental variables

Thesis for the *cand. scient.* degree in fisheries biology

by

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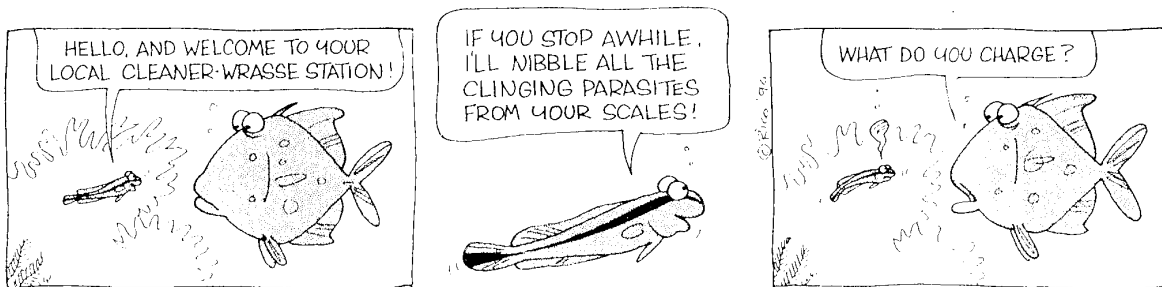


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Department of Fisheries and Marine Biology

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For my mother,
Aud Hauge Thangstad-Lien
(1927-1990)



('Sea People' by Rico, DIVER Magazine)

ABSTRACT

Wrasse (Pisces: Labridae) were formerly a largely unexploited fish group in Norway, but during the last decade some labrid species have been increasingly utilised as cleaner-fish in salmon culture. The growing fishery for cleaner-wrasse has actuated the need for more knowledge about labrid ecology. In this study the occurrence and abundance of three common cleaner-wrasse species on the Norwegian West coast was analysed in relation to spatial and environmental variables at 20 shallow water study sites in Masfjord.

Analyses were based on catch data of goldsinny (*Ctenolabrus rupestris* L.), rock cook (*Centrolabrus exoletus* L.) and corkwing wrasse (*Symphodus melops* L.), obtained from the Masfjord 'cod enhancement project' sampling programme. Data were used from monthly sampling by beach seine on 10 of the study sites (299 stations in total) and by a net group consisting of a 39 mm meshed gillnet and a 45 mm meshed trammel-net at all 20 sites (360 stations in total), July 1986-August 1990. The habitat-related variables substratum type, substratum angle, dominating macrophytic vegetation, and degree of algal cover at each study site were recorded by scuba. The degree of wave exposure was estimated from chart positions of the study sites. Temperature and salinity were measured regularly as part of the beach seine sampling (174 out of 299 stations). Habitat types were classified based on matching levels of the habitat variables, and consisted of sheltered or exposed rocky shore, mudflats and kelp forest. Analyses were done by means of generalised linear ANOVA and regression models (GLMs), where a binomial error distribution was assumed for the frequency data, and Poisson or negative binomial errors for the abundance data.

The catch-frequency distributions were all highly aggregated, especially for rock cook, with high variance-to-mean ratios and low values of the dispersion parameter k . Beach seine samples were dominated by goldsinny (55% of total catch), while rock cook were highly dominant in the gillnet samples (78%) and corkwing partly dominant in the trammel-net samples (47%). Net catches consisted entirely of adult (I+ group) individuals larger than 8-10 cm, whereas up to 85% of the individuals in the beach seine catches were 0 group juveniles less than 5 cm. The availability of wrasse to capture was highly dependent on season, with low catch rates until May, and peaks in July-August. Except for a 1988 abundance peak for both juveniles and adults of all species in the beach seine catches, there were no differences in catch rates between years.

Catch analysis showed an apparent ontogenetic shift in spatial use for goldsinny, with 0 group being most common in the outer parts of the study area adjacent to neighbouring Fensfjord, whereas older goldsinny were increasingly common towards the inner parts of Masfjord proper. For rock cook no significant spatial differences with regard to subarea were found, while corkwing occurred overall most frequently in the outer fjord area. For the beach seine samples no association with habitat was evident, but in net samples goldsinny and rock cook were most common on rocky shore habitat. Presence of broken rock appeared to be the main factor explaining the distribution of these two species. Beach seine catches of corkwing seemed mainly affected by the degree of algal cover. The activity of wrasse is thought to be mostly dependent on water temperature; the temperature effect was thus generally high for all species, and explained up to half of the catch rate variation. Age 0 corkwing appeared to be positively influenced by increasing temperature as well as increasing salinity, although the effect of both factors was comparably low for these individuals.

SAMMENDRAG

(in Norwegian)

Leppefisk (Pisces: Labridae) var tidligere en lite utnyttet fiskegruppe i Norge, men endel arter har i løpet av det siste tiåret i økende grad blitt benyttet til avlusing av oppdrettslaks. Det økte fisket etter leppefisk har aktualisert behovet for større kunnskap om leppefiskenes økologi. I dette arbeidet blir forekomster og mengder av tre vanlige leppefiskarter på vestkysten av Norge analysert i relasjon til miljøvariabler på 20 gruntvannslokaliteter i Masfjorden.

Analysene ble gjort på grunnlag av fangstdata av bergnebb (*Ctenolabrus rupestris* L.), grasgylt (*Centrolabrus exoletus* L.) og grønngylt (*Symphodus melops* L.), innsamlet i forbindelse med Masfjordprosjektets 'Torsk i fjord'-program. Det ble brukt data fra månedlig prøvefisking med strandnot på 10 av studielokalitetene (299 stasjoner totalt), og med en garngruppe bestående av et auregarn (39 mm strekt maskevidde) og et trollgarn (= sildegarn, 45 mm strekt maskevidde) på alle 20 studielokalitetene (360 stasjoner totalt), juli 1986-august 1990. De habitatrelaterte variablene substrattype, substratvinkel, dominerende makrofytt-arter og algedekningsgrad ble registrert ved apparatdykking (scuba) på hver lokalitet. Bølgeeksponeringsgraden ble vurdert ut fra hver lokalitets kartposisjon. Temperatur og salinitet ble målt regelmessig i forbindelse med strandnotprøvetakingen (174 av 299 stasjoner). Habitattyper ble klassifisert på grunnlag av likheter i habitatvariabelnivåene, og bestod av skjermet eller eksponert hardbunns habitat, bløtbunns habitat og tareskog. Fangstene ble analysert ved hjelp av generaliserte lineære ANOVA- og regresjonsmodeller (GLMs) hvor den binomiske fordeling ble brukt som feilledd for frekvensdataene og Poisson- eller negativ binomial-fordeling for mengde-dataene.

Frekvensfordelingene av fangstene var meget aggregerte, spesielt for grasgylt, med høy varians og lav forventning, og lave verdier av negativ binomial-parametere k . Bergnebb dominerte i strandnotfangstene (55% av totalfangsten), grasgylt i auregarnfangstene (78%), mens grønngylt tildels dominerte sildegarnfangstene (47%). Garnfangstene bestod kun av voksne (I+) individer større enn 8-10 cm, mens opptil 85% av strandnotfangstene var av juveniler (nullgruppe) mindre enn 5 cm. Fangsttilgjengeligheten av leppefisk var meget sesongavhengig, med lave fangstrater t.o.m. april, og fangsttopper i juli-august. Gjennomsnittlig fangstrate var tilnærmet lik for hvert år i prøvetakingsperioden, bortsett fra en fangsttopp for både juveniler og voksne individer av alle artene i strandnotprøvene fra 1988.

Fangstanalyser av bergnebb viste et øyensynlig ontogenetisk skifte i romlig assosiasjon, hvor juveniler forekom hyppigst i det ytre området mot Fensfjorden, mens eldre bergnebb var vanligere mot de indre delene av området, innenfor selve fjordterskelen. Ingen signifikante romlige forskjeller m.h.t. delområde ble funnet for grasgylt, mens grønngylt jevnt over var mest vanlig i prøver fra det ytre området. Det kunne ikke påvises habitatassosiasjon for individer i strandnotprøvene; i garnprøvene var bergnebb og grasgylt derimot mest vanlig på hardbunns habitat. Nærvær av steinur syntes å påvirke fordelingen av disse to artene mest. Strandnotfangster av grønngylt syntes å være mest påvirket av graden av algetetthet. Leppefiskenes aktivitet er sannsynligvis i stor grad avhengig av sjøtemperaturen; temperatureffekten var således stor for alle artene og forklarte opptil halvparten av variasjonen i fangstene. Nullgruppe grønngylt syntes å være positivt påvirket både av økende temperatur og økende salinitet, men effekten av begge faktorene var relativt lav for disse individene.

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1 INTRODUCTION

Several species of the wrasse family (Pisces: Teleostei: Labridae) are very common in Norwegian inshore waters, but these have traditionally not been considered a commercially valuable resource (Wheeler 1969). This changed in 1987 when it was discovered that some wrasse species could act as cleaner-fish in salmon farming (Bjordal 1988). Since then a new fishery for cleaner-wrasse has caused renewed interest in their largely unknown ecology.

Cleaning symbiosis - in which the cleaner-fish removes parasites from the skin of other fish - is well-known in tropical reef wrasse, but was for temperate wrasse like the goldsinny (*Ctenolabrus rupestris* L.) formerly only observed in aquarium setups (Potts 1973) and on some occasions in the field (Hilldén 1983). This seemingly innate labrid cleaning behaviour was tested with farmed salmon (*Salmo salar* L.) in tank trials at the Institute of Marine Research (IMR) in Bergen, where especially goldsinny and rock cook wrasse (*Centrolabrus exoletus* L.) showed good cleaning ability (Bjordal 1988, 1990). Corkwing wrasse (*Symphodus melops* L.) also showed cleaning behaviour, but were subject to high mortality in the initial trials (Bjordal 1992). All three species are currently widely used in salmon farms in Norway, Scotland and Ireland to effectively control ectoparasites like salmon louse *Lepeophtheirus salmonis* (Krøyer), as a supplement to traditional treatment with nerve toxins (Bjordal 1992).

The demand for cleaner-wrasse in salmon farming in Norway has been steadily increasing; from some 50.000 individuals in 1989 to 1.5-2 million individuals in 1995 (Bjordal 1999). It is estimated that in 1998 in excess of three million individuals, mainly goldsinny, rock cook and corkwing wrasse, were used for this purpose. The main fishery for wrasse takes place on the Norwegian west coast with traps, pots and fyke nets from May to October (Bjordal 1993). The increasing fishing pressure has caused concern about the possible impact on local wrasse populations (Darwall *et al.* 1992, Skog 1994, Skog *et al.* 1994, Costello 1996). Data from Ireland already indicate

that intensive fishery may change population structure through selective removal of larger fish, especially corkwing males (Darwall *et al.* 1992).

Although the cleaner-wrasse species introduced above are highly abundant along most of the coastline of Europe, not much is known about their ecology. The rock cook in particular is a poorly studied species. In Norway, data on the ecological distribution of these and other wrasse were formerly limited to a few faunistic surveys (e.g. Tambs-Lyche 1954, 1987). The number of recent surveys including ecological data on wrasse is, however, growing. In particular, the so-called 'cod enhancement project' in Masfjord necessitated an extensive multi-species sampling programme over several years (1986-1992) (Smedstad *et al.* 1994, Alvsvåg 1993). Shorter-term surveys include Andersen *et al.* (1993), Høisæther & Fosså (1993), Johannessen (1993, 1994), and Skog *et al.* (1994). Distributional studies have also been conducted in Sweden (Hilldén 1984), Scotland (Sayer *et al.* 1993) and Ireland (Darwall *et al.* 1992). Reviews of current knowledge about the ecology and life history of wrasse are given in Costello (1991), Darwall *et al.* (1992), Sayer *et al.* (1996) and Hjohlman (1996).

Despite the growing number of works on wrasse biology and ecology, the amount of available information remains severely deficient (Costello 1991, Darwall *et al.* 1992, Hjohlman 1996). Further quantitative data on the ecological importance of wrasse, with respect to for example abundance, distribution and resource preferences, would therefore be essential in order to assess the impact of the growing commercial exploitation (Costello 1991, Hjohlman 1996). My primary aim for this study is thus to evaluate to which extent habitat preferences and variables of the physical environment that determine the habitat affect the local distribution of goldsinny, rock cook and corkwing wrasse.

Many factors may limit the extent to which fish and other animals are distributed. A number of these factors were summarised by Krebs (1985, p. 39) into a hierarchical chain. Proceeding sequentially down this chain one starts with animal dispersal, which will generally act in aiding a species' recruitment to new areas, thereby increasing its potential range of distribution. Examples of dispersal in wrasse are the passive transport of pelagic eggs and larvae of some species, for example goldsinny (Hilldén

1984), by currents, and also winter migrations to deeper water, which have been reported for some species (e.g. Hilldén 1984). The next step in the chain is the selection of a suitable habitat. Habitat selection will often tend to limit a species' distribution within its range of dispersal. Inter- and intra-specific competition and predation, as well as environmental factors like temperature, salinity, exposure and currents may further limit its distribution. Temperature is likely to be an important limiting factor for a group of basically warm water species such as wrasse, and has been reported as a triggering factor for winter migrations of the North-American labrid *Tautoga onitis* (Olla *et al.* 1980). The importance of habitat selection, temperature, salinity and other variables as factors in determining the distribution of wrasse are considered and discussed in this thesis.

Selection is defined (Johnson 1980) as a process in which an animal actually chooses a component such as habitat, and is said to occur if the component is used disproportionately to its availability. The process of habitat selection is poorly understood (Krebs 1985). Von Uexküll (1921) relates it to the animal's sensory perception of its *Umwelt* (i.e. the sum of its surroundings, or its habitat). Features of this *Umwelt*, e.g. habitat characteristics, may thus trigger a psychological preference or choice in the animal (Klopfer 1969). *Preference* is defined as the likelihood of a given component being chosen if offered on an equal basis with others (Johnson 1980). For this reason habitat preferences are probably better studied in experiments where the habitat variables are deliberately altered in order to determine an animal's response (Ramsey *et al.* 1994). For observational studies such as the present one, it would seem more suitable to use terms like *association* or *correlation*, which do not imply an active choice by the animal.

Various, mostly rather vague, definitions of habitat have been given, e.g. '... the place an animal lives or where one would go to find it ...' (Odum 1971, p. 234), '... an area which seems to possess a certain uniformity with respect to physiography, vegetation, or some other quality ...' (Andrewartha and Birch 1961, p. 28). To avoid confusion with the closely related concept of an animal's *ecological niche*, Whittaker *et al.* (1973) suggest that *habitat* should apply to the range of environments (or communities) over which a species occurs, whereas *niche* should apply to the intra-

community role of the species. This concept of habitat is further described as an m -dimensional hypervolume, in which ' m variables of the physical and chemical environment that form spatial gradients in a landscape or area define as axes a habitat hyperspace'. The species' distributional response to factors within this hypervolume then describes its habitat.

For this habitat study I used abundance data of goldsinny, rock cook and corkwing wrasse, obtained through sampling during the 'cod enhancement project' of the IMR (1985-1992). Known mostly as the 'Masfjord project', this survey attempted to analyse the possibilities for enhancement of a natural fjord population of cod by releasing pond reared juveniles (Smedstad *et al.* 1994). To better understand the effects such a large scale release of reared juveniles might have, a preliminary study of the fjord ecosystem was necessary. A monthly experimental sampling programme was therefore started in order to collect data on the composition and distribution of stocks of wild cod and its predators and competitors. Wrasse form one of the numerically most important groups of fish in shallow water after gadids (Salvanes & Nordeide 1993), and are represented in large numbers in the catches. Moreover, Masfjord is a well-studied fjord with respect to hydrography (Aure 1978, Aksnes *et al.* 1989), topography and vegetation (Fjeldstad 1991), and benthic and pelagic fish and other animals (Salvanes 1986, Aksnes *et al.* 1989, Giske *et al.* 1990, Fjeldstad 1991, Alvsvåg 1993, Salvanes & Nordeide 1993, Salvanes *et al.* 1995).

In summary, the objectives of the present study are

- to describe the temporal and spatial distribution of goldsinny, rock cook and corkwing in Masfjord,
- to describe their habitat with respect to variables (factors) of the physical environment, and
- to consider and discuss the effect these factors have on the occurrence and abundance of the species.

2 MATERIALS & METHODS

2.1 The species

Wrasse (Teleostei: Labridae) form a large family (about 500 species, Nelson 1984) of marine perciform fishes, which are distributed in tropical, warm temperate and temperate waters around the world. In Norway, Ballan wrasse (*Labrus bergylta* Ascanius), cuckoo wrasse (*L. bimaculatus* L.), goldsinny (*Ctenolabrus rupestris* L.), rock cook (*Centrolabrus exoletus* L.) and cork-wing wrasse (*Symphodus* [*Crenilabrus*] *melops* L.) are commonly found in shallow water along the coast north to Trondhjemsfjord (c. 63° N) (Wheeler 1969). The scale rayed wrasse *Acantholabrus palloni* (Risso) is a deep-water species (50-270 m) (Wheeler 1969), and has only been recorded on a few occasions in Norway (Pethon 1966, Fosså *et al.* 1989).

The following information on the biology and life-history characteristics of the study species is, if not stated otherwise, taken from Wheeler (1969), Hilledén (1984) and Costello (1991).

2.1.1 Goldsinny

A slim-bodied and small species, (Jago's) goldsinny rarely grows larger than 12 cm (Table 1). Maximum age is generally given as 6 years (Table 1), but Sayer *et al.* (1996) report 14+ and 20+ years old males and females, respectively. Adults are orange to red in colour, juveniles may be dull green. The most distinctive feature is a black 'eye-spot' on the base of the tail-fin (Figure 1), which is thought to aid in species recognition. Goldsinnies are essentially monochromatic; apart from some reddish spots along the flanks of the male the sexes are not easily distinguishable visually. Functional 'accessory males' with female secondary characteristics occur. Unlike many other labrids (e.g. Ballan and cuckoo wrasse), the studied species are all gonochoristic, and thus do not change sex (e.g. protogynous hermaphroditism). Both sexes of all three study species mature at about age 2 years. Mature goldsinny males occupy small (1.5-2.0 m²), permanent territories, which are defended vigorously during the reproductive

Table 1 - Comparison of some growth and life-history characteristics of the study species. Table modified from Hilledén (1984) and Darwall *et al.* (1992).

Species	Goldsinny	Rock cook	Corkwing
Maximum age	6 yr	8 yr	9 yr
Age at maturity (female)	2 yr	2 yr	2-3 yr
Growth rate to maturity	3.0 ± 1 cm yr ⁻¹	4.0 ± 1 cm yr ⁻¹	3.0 ± 1 cm yr ⁻¹
Maximum size	18 cm (mostly < 12 cm)	15 cm (mostly < 12 cm)	28 cm (mostly < 16 cm)
Size at age 1 [†]	4.0 - 4.7 cm	5.5 - 5.8 cm	5.7 - 7.0 cm
Size at maturity	9.5 cm	Unknown	10 cm
Diet	Crustacea/Mollusca	Unknown	Mollusca
Spawning season	April-September	May-August	April-September
Spawning place	Mid-water	Nest?	Nest of algae
Spawning mode	Batch	Unknown	Batch
Parental care	None	Unknown	Male
Egg type	Pelagic	Benthic	Benthic

[†] Female - male (Quignard 1966).

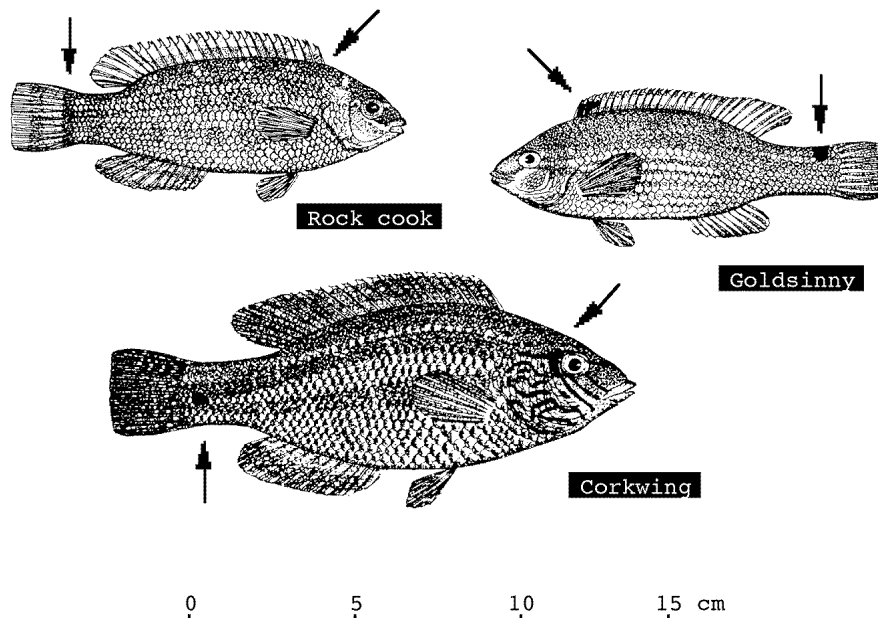


Figure 1 - Study species: wrasse typically have a perchlike body form, spiny fin rays, and a highly protrusible mouth with fleshy lips. The scale shows each species at its normally attained maximum size (see Table 1). Arrows point to characteristic markings (see text). Drawings from Whitehead *et al.* (1986).

season, which lasts from May to June in Nordic waters. When densities are high, non-territorial goldsinny aggregate in shoals above more marginal substrata. Reproduction is polygynous and lek-like. Pair-wise spawning and batch-wise release of the eggs occurs in mid-water above each territory. Most of the non-sticky eggs descend to the bottom, but about 10% are carried away by currents. The goldsinny is an opportunistic feeder on a variety of benthic invertebrates depending on availability. Its most important food items appear to be gastropods and amphipods, but it also specialises to some extent on tearing off bryozoans and hydrozoans from kelp leaves with its strong forward-pointing teeth.

2.1.2 Rock cook

Sometimes known as small-mouthed wrasse, rock cook are about the same size as or somewhat smaller than goldsinny (Table 1). Maximum age is reported to be 8-9 years (Treasurer 1994), although Alvsvåg (1993) found 12-13 year old specimens in Masfjord. Colouration varies from greenish-brown to reddish, with stripes on the head region. The scales of the male often show an iridescent blue colouration, which intensifies during the spawning season, otherwise there is no dependable way of distinguishing between the sexes. Other features include two broad, dark bands, one at the root of the caudal fin, the other on the dorsal fin (Figure 1). Territorial behaviour in rock cook has been observed during the spawning season. After spawning the fish leave their territories and aggregate in shoals (pers. obs.). The spawning behaviour of the rock cook is unknown, but the male or female is thought to build a nest for the eggs. Like the goldsinny this species is an opportunistic feeder, but it also specialises to some extent on small polychaetes like *Pomatoceros triqueter*.

2.1.3 Corkwing

Corkwing are slightly larger (Table 1) and deeper-bodied (Figure 1) than the other two species. Maximum age is given as 6-9 years (Darwall 1992, Alvsvåg 1993, Sayer *et al.* 1996). Colouration varies with habitat, season, sex and maturation (Lythgoe & Lythgoe 1991), but is usually a dull green to greenish-brown for females and juveniles, whereas males are more reddish-brown. The males show red and blue striping on the lower head and stomach

regions, especially during the reproductive season. Distinguishing features are a spot on the caudal peduncle on or just below the lateral line, and a crescent-shaped spot behind the eye (Figure 1). The male corkwing uses algae to build an egg-guarding nest. Pair-spawning may take place with several females. The corkwing takes a large variety of prey, mainly bivalves and copepods (Alvsvåg 1993).

2.2 The fjord

The study was conducted on locations in Masfjord and parts of Fensfjord (Figure 2). Masfjord is situated *c.* 50 km to the north of Bergen (60°50'N 5°25'E), western Norway, extending as a side arm from the larger Fensfjord, through which it is connected to coastal waters. Masfjord is a typical fjord of the western region of Norway, with a deep middle region (494 m) and a shallow sill (75 m) (Giske *et al.* 1990), formed by ice age glacier erosion. It is about 22 km long, with a shoreline of *c.* 70 km and a width ranging from 0.3 to 1.5 km (Salvanes & Nordeide 1993). The sill forms the boundary with Fensfjord.

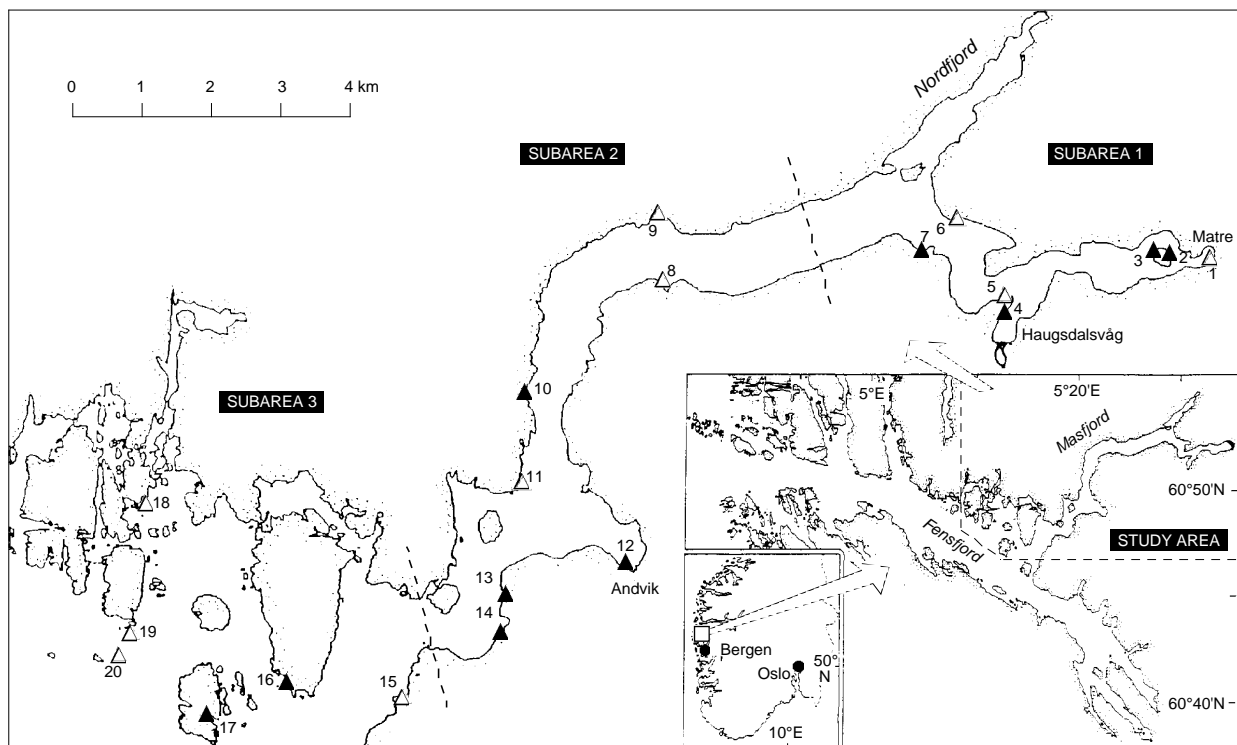


Figure 2 - Study area with sampling sites. [△] beach seine and net sampling; [▲] net sampling only. The fjord sill is located at the boundary between subareas 2 and 3 (boundaries are indicated by dashed lines).

2.2.1 Topography

The study area can be divided into three topographically different subareas (Figure 2): inner (subarea 1), central (subarea 2) and outer fjord area (subarea 3). Both subareas 1 and 2 (i.e. Masfjord proper) are surrounded by up to 700 m high mountains. Subarea 2 has steep and rocky sides, whereas subarea 1 is somewhat less steep with an overall substratum angle averaging about 45° (Fjeldstad 1991). The deepest parts of the fjord, extending to about 500 m, are found in subarea 2. Two large bays are of importance, Haugsdalsvåg in subarea 1 and Andvik in subarea 2. The bottom at the river estuaries in Andvik is muddy, while the outer parts consist of sand and gravel. Haugsdalsvåg is completely covered by a muddy substratum. Both bays have a gradually inclining substratum angle. Subarea 3, from the sill westwards into neighbouring Fensfjord, is generally shallower than the other two areas, with depths ranging from 50 to 200 m, and is characterised by a number of small islands, islets and bays with a sandy bottom. Nordfjord, stretching north in subarea 1, has a shallow sill and little exchange of the mostly anoxic basin water.

2.2.2 Hydrography

A brackish water layer 1 to 3 m deep is found all year round in Masfjord (Aure 1978), and is caused by constant freshwater runoff from the hydroelectric power plant at the head of the fjord in Matre (Figure 2). During winter this runoff creates ice-free conditions along the main fjord axis (Smedstad 1991). Freshwater influx to the fjord varies between 30 and 60 m³ s⁻¹ and amounts to about 0.1% of the total fjord volume per day (Aksnes *et al.* 1989). Temperatures in the brackish water layer range from 2-5°C in the winter to 12-17°C in the summer. An intermediate water layer is found between the brackish water and the sill (3-75 m), and deep water is found below the sill. The intermediate layer can be divided into coastal water (salinity below 34.5¹, temperatures 8 to 15°C) and Norwegian Trench water (salinity above 34.5¹, temperature 7-8°C) (Aksnes *et al.* 1989). Tidal amplitude in Masfjord is 0.5 to 1 m, and daily exchange due to tide is about 0.5% of the total fjord volume. Incidences of coastal down- or upwelling, mainly driven through periods of prevailing southerly or northerly winds,

¹ Salinity (S) in psu (practical salinity units, as defined in IAPSO 1985)

force rapid water exchanges in the upper part of the intermediate layer (Aksnes *et al.* 1989).

2.2.3 Aquatic vegetation

The Masfjord littoral (above low tide level) is dominated by furoid weeds like *Fucus serratus*, *F. vesiculosus* and *Ascophyllum nodosum*. Below the low tide level kelp algae like *Laminaria digitata*, *L. hyperborea* and *L. saccharina* are found, together with *F. serratus*, *Halidrys siliquosa* and eel grass *Zostera marina*. Kelps are for the most part patchily distributed, except on exposed outer locations, where *L. hyperborea* is found with up to 10 individuals m^{-2} (Fjeldstad 1991). In the archipelago facing Fensfjord *Laminaria* spp penetrate down to *c.* 26 m (Fosså 1991). *L. saccharina* is found in all subareas at depths below 5 m. *Z. marina* is mainly found on sheltered localities in the central and outer subareas. The number of occurring macrophyte species increases towards the outer fjord areas (Fjeldstad 1991).

2.3 Study sites

Study sites were selected among beach seine and net sampling locations used during the Masfjord Project (see Introduction).

Beach seining was conducted on a monthly basis - mainly for 0 group cod and small shallow water prey fish like gobies (Smedstad *et al.* 1994) - on 10 *fixed* locations (Appendix 1) suitable for the deployment of a seine. This precluded some of the steeper sections of the Masfjord shoreline. All of the beach seine locations were included as study sites in this thesis (Figure 2).

Net sampling was conducted monthly at about 5-20 m depth, mainly for larger predators like cod and other gadoids (Salvanes & Ulltang 1992). About twenty net groups were set at *random* on all known cod habitats within each subarea (Salvanes 1991, Salvanes & Ulltang 1992). For this study I have used data from nets set on positions approximately corresponding to the positions of the ten beach seine sampling locations, as well as data from ten other sampling locations that were sampled at least 10 times by the nets (Figure 2, Table 2, Appendix 1). Sampling data from November and December

1987, April 1989 and April 1990 were excluded from analysis, because a different net sampling strategy was used. Site no. 17 was disregarded, because it was only sampled once. Hence, the number of net samples considered in this study varied to some extent between sites and years (Table 2).

2.4 Sampling gears and procedures

2.4.1 Beach seine

Beach seine samples were collected during daylight hours on two consecutive days of each month. The gear was mostly handled by the same two operators (J.H. Fosså, pers. comm.). About 7 m of shoreline was sampled in one haul, to depths between 5 and 10 m. The seine was 4 m deep, 40 m long and had a 5 mm mesh size (knot-to-knot) netting, except for the mid-part, which was 8 m long with 3 mm round mesh openings (Fosså 1991).

2.4.2 Net group

The gillnet and the trammel-net were bottom-set *c.* 30 m apart, perpendicular to the shore, with surface buoys at the shallow ends. The nets were set during the afternoon and retrieved the following morning. Sampling was spread over four consecutive nights, one per subarea with an additional night in each subarea every third month. Setting and retrieval time were recorded (Appendix 3) for determination of the fishing period (soak time). The average fishing period was about 18 hours. The fishing depth range was estimated by echo sounding at the points where the net ends were dropped from the boat. The range was on average between 5 and 20 m (Figure 3). The shallow ends of the nets were normally dropped at 0-6 m depth, but were on a few occasions set deeper (8-25 m depth), resulting in a correspondingly greater range for some sites (Figure 3).

The net group consisted of:

- i) a single panel gillnet, 25 m long and 2 m deep, with 39 mm stretched mesh, made of 0.2 mm monofilament and with a hanging ratio of 1:3;
- ii) a triple panel trammel-net, 28 m long and 2 m deep, with an inner net

Materials & methods

Table 2 - Number of beach seine hauls and net settings per site and per season during the study period. [-] no sampling.

Site no.	1986		1987		1988		1989		1990		Total
	Win	Sum	Win	Sum	Win	Sum	Win	Sum	Win	Sum	
Beach seine											
2	2	1	2	5	3	5	3	3	1	5	30
3	2	-	2	5	3	5	3	3	1	5	29
4	2	-	2	5	3	5	3	3	1	5	29
7	2	2	2	5	3	5	3	3	1	5	31
10	2	1	2	5	3	5	3	3	1	5	30
12	2	1	2	5	3	5	3	3	1	5	30
13	2	1	2	5	3	5	3	3	1	5	30
14	2	1	2	5	3	5	3	3	1	5	30
16	2	1	2	5	3	5	3	3	1	5	30
17	2	1	2	5	3	5	3	3	1	5	30
Total	20	9	20	50	30	50	30	30	10	50	299

Nets											
1	2	2	2	3	4	4	5	3	2	2	29
2	-	-	-	-	3	2	1	-	2	-	8
3	5	5	4	4	4	2	4	2	2	4	36
4	1	3	2	2	-	1	1	2	-	2	14
5	2	1	3	4	4	3	1	3	1	-	22
6	3	3	3	3	2	2	2	2	-	-	20
7	-	-	2	3	1	2	-	2	-	1	11
8	3	4	3	3	3	4	3	4	3	2	32
9	1	1	1	1	2	3	3	1	-	1	14
10	2	2	1	2	2	2	2	2	1	-	16
11	2	2	2	5	2	3	3	3	-	-	22
12	3	1	2	5	3	1	2	2	-	2	21
13	3	2	2	2	2	2	2	1	4	4	24
14	-	1	-	1	1	1	-	2	-	1	7
15	1	2	2	1	3	3	2	3	1	-	18
16	1	3	2	1	1	2	-	1	2	2	15
18	2	-	3	3	4	2	3	2	-	2	21
19	-	2	1	3	-	2	-	2	-	1	11
20	3	4	2	2	3	1	2	-	1	1	19
Total	34	38	37	48	44	42	36	37	19	25	360

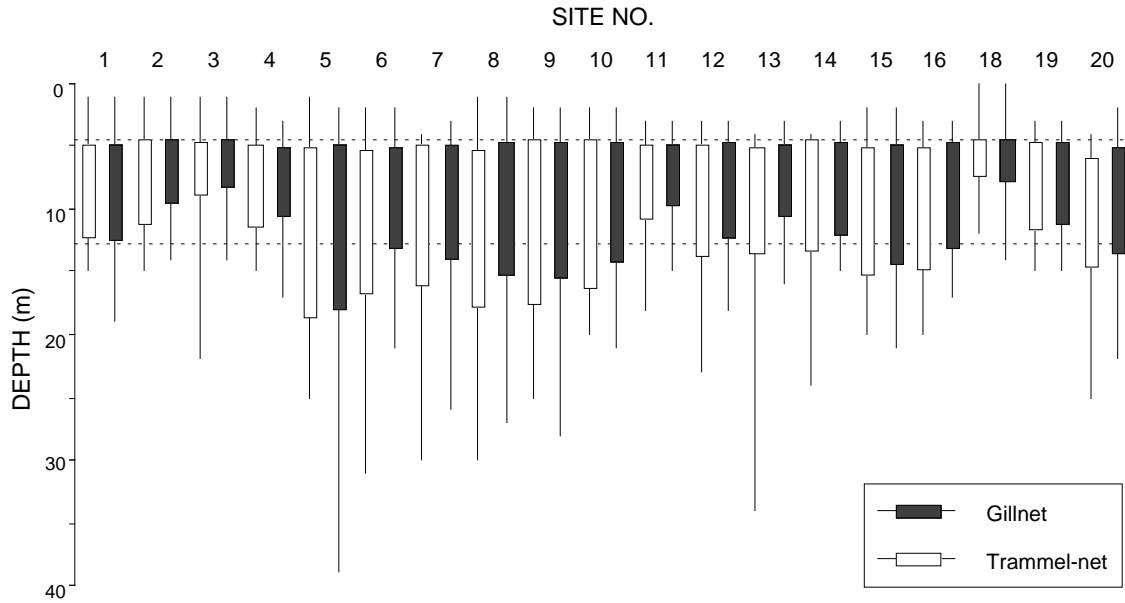


Figure 3 - Minimum and maximum depth (thin bars), and mean depth (thick bars) at the shallow and deep net ends of the nets. Dashed lines indicate the overall depth range.

stretched mesh size of 45 mm and 261 mm stretched mesh in the outside nets, a hanging ratio of 1:3 and made of nylon twine.

A 70 mm mesh trammel-net was also used during the sampling project, but this gear caught so few wrasses that I have disregarded it. In the following data analysis the catch data from the gillnet and the 45 mm trammel-net were combined (pooled).

2.5 Sample treatment and measurements

The beach seine samples were fixed in 4% neutralised formaldehyde within 30 minutes after capture. After species determination and measurement of total sample weight of each species (nearest 0.1 g) the samples were preserved in 75% ethanol and stored. Lengths of individuals in the majority of the samples were after storage measured by myself (total length, nearest 0.5 cm below). The species sample weight and mean fish length for each species in each sample is given in Appendix 2.

The net samples were preserved in ice. Later individual fish were measured to the nearest cm below (total length, TL). Weight was measured to the

nearest g. For some (large) samples only the total sample weight was measured. The mean fish length for each species in each sample is given in Appendix 3.

The length composition of samples for which only the total sample weight per species was measured, was estimated (Appendix 2)

i) for one-specimen samples where sample weight = individual weight: using the length-weight relationship obtained from measured samples:

$$\hat{l} = a \cdot w^b \quad (\text{Ricker 1973}),$$

where \hat{l} is the length to be estimated, w is the (sample) weight, and a and b are coefficients found by linear regression on:

$$\log(\hat{l}) = \log(a) + b \cdot \log(w);$$

ii) for the remainder of the samples, length compositions for each quarter of each year were assumed equal to pooled length-frequencies from measured samples from the same quarter.

2.6 Environmental variables

A number of habitat-related characteristics of the study sites were surveyed by scuba diving during August 1991. The variables substratum type, angle of the substratum, macrophyte species and macrophyte cover availability were visually estimated while diving along three parallel transects placed perpendicular to the shore (i.e. vertical transect). The first transect was placed through the approximate centre of the shoreline stretch sampled by the beach seine or by the nets, thereafter two transects were placed about 20 m to each side of this position. With underwater visibility varying from 5 to 10 m, a shoreline of 50 to 60 m could roughly be surveyed visually. Transect length was restricted to 30 m by the diver-to-surface communication cable which was operated from the shore. Three divers including myself were used, each alternately operating the communication line, recording data and diving.

Table 3 - Classification of substratum types found in Masfjord.

Substratum type	Particle size and texture	Variable name
Mud, sand	Fine (<1 mm) to grainy (<5 mm) particles	Soft bottom
Gravel, pebbles, rubble	Coarse objects less than <i>c.</i> 5 cm	Rubble bottom
Cobbles, boulders, blocks	Coarse objects larger than <i>c.</i> 5 cm	Broken rock
Bedrock, rock flats	Large, relatively smooth surfaces	Smooth rock

2.6.1 Substratum type

Substratum type was classified according to particle size (Table 3). The percentage frequency of each substratum type was calculated as the percentage of transect intervals along which it was recorded, and converted to one of 4 ordinal variable levels (Appendix 4):

Level 1 (absent):	0
Level 2 (patchy):	1-20%
Level 3 (medium):	21-50%
Level 4 (abundant):	51-100%

2.6.2 Substratum angle

The angle of the substratum along each transect interval was calculated using the depth Z and the distance L at each interval stop i :

$$\text{Angle} = \sin^{-1}(Z_i/L_i).$$

The overall (mean) angle at each site was converted to one of three ordinal variable levels (Appendix 4):

Level 1 (slight):	< 10°
Level 2 (moderately steep):	11-25°
Level 3 (very steep):	> 25°

2.6.3 Macrophyte cover availability

The presence of the macrophytic species *Fucus serratus*, *F. vesiculosus*, *Ascophyllum nodosum*, *Laminaria digitata*, *L. hyperborea*, *L. saccharina*, *Halidrys siliquosa* and *Zostera marina* was recorded along each transect. The frequency of occurrence of each species was calculated as the percentage of transect intervals along which it was observed, and converted to one of four ordinal variable levels as in section 2.6.1 (Appendix 5).

The percentage bottom area covered by macrophytes regardless of species was visually estimated along each transect interval, using percent-frequency levels as defined in section 2.6.1. The overall level of cover availability at each site was calculated as the median level over all estimates (Appendix 4).

2.6.4 Exposure

An index of the degree of wave exposure at each study site was obtained from an indirect method proposed by Baardseth (1970) by counting from the exact position of a site on a chart the number of sectors n of a given radius that contain only open sea. The number obtained - in this case $n \leq 40$ (i.e. 9° radius) - is assumed correlated with the degree of exposure at a site (Appendix 4):

Level 1 (sheltered):	no sectors
Level 2 (semi-exposed):	1-7 sectors
Level 3 (fully exposed):	8-40 sectors

A sector radius of 7.5 km as used by Baardseth (1970) would classify all sites as sheltered; it was therefore reduced to 3.75 km.

2.6.5 Temperature and salinity

Temperature and salinity were measured semi-regularly on the beach seine sampling stations ($n = 174$), using a Model 5005 Kent Oceanography Measuring

Bridge. Measurements were taken at 1-5 m intervals to a depth of about 25 m. Mean values per site are given in Appendix 2.

2.7 Habitat classification

Based on the levels of the habitat-related variables measured during the diving survey, and including the degree of exposure at each site, a similarity matrix between the study sites was computed (Appendix 6) using a modification of Jaccard's coefficient for ordinal variables (Gordon 1981):

$$s_{ij} = \frac{2a}{2a + b},$$

where a represents the frequency of matches and b the frequency of mismatches between variable levels for sites i and j . Matching levels were given double weight as in Johnson & Wichern (1992). Co-absences of a variable level were excluded.

Cluster analysis (e.g. Digby & Kempton 1987, Jongman *et al.* 1995) was used on the resulting matrix as an aid in identifying groups of sites with a similar habitat type. Cluster or agglomerative hierarchical methods work on a matrix of similarities between a set of units - in this case the study sites - linking those units that are most similar into groups or clusters. These clusters are then treated as single units and linked with the next-most similar unit. The technique of group-average linking, which is widely used in ecology (Jongman *et al.* 1995), was applied to the data.

2.8 Data analysis

The environmental variables defined above were used as potential explanatory factors for the occurrence and abundance of the study species in the samples. The analysis was done by means of generalised linear modelling (McCullagh & Nelder 1989, Aitkin *et al.* 1989), using the statistical software package *GLIM* (Generalized Linear Interactive Modelling; Payne 1986, Aitkin *et al.* 1989, Crawley 1993).

Generalised linear models (GLMs) are an extension of the classical linear model, and are defined by:

i) a *random* component \mathbf{Y} , independently distributed with mean $E(\mathbf{Y})=\boldsymbol{\mu}$ and constant error variance. The distribution of \mathbf{Y} may be derived from any of the exponential families, including the normal, Poisson, binomial, geometric and negative binomial.

ii) a *systematic* component $\boldsymbol{\eta}$, the linear predictor:

$$\boldsymbol{\eta} = \sum_{j=1}^p \mathbf{x}_j \beta_j,$$

where x_j are the model variates and β_j the model parameters.

iii) a *link function* $g(\cdot)$ between the random and the systematic component:

$$\eta_i = g(\mu_i),$$

where g may become any monotonic differentiable function (McCullagh & Nelder 1989).

In the classical linear model the error term (i) is normally distributed, and the link function (iii) equals identity:

$$\boldsymbol{\eta} = \boldsymbol{\mu}.$$

For counts like the present catch-per-unit-effort data this is clearly not appropriate, since it could lead to the prediction of negative numbers in the catches. Instead a log link function was used so that $\mu > 0$, while a Poisson or negative binomial error term takes into account that the data are integer and have variances respectively equal to or varying with the mean.

Frequency distributions of abundance data from marine surveys are often highly skewed to the right, with a large proportion of zeros and a high variance-to-mean ratio (Pennington 1996). Aggregated or 'contagious' distributions like this are frequently well approximated by the negative binomial (NB) (Southwood 1966, Power & Moser 1999). The shape of the NB distribution is determined by k , the dispersion parameter. An estimate of k less

than 1 indicates a large extent of overdispersion or aggregation, suggesting that the NB may provide a good fit to the data. As $k \rightarrow \infty$ the distribution approaches a Poisson distribution, as $k \rightarrow 0$ it approaches the logarithmic series. The fit of the NB to the observed catch-frequency distributions was estimated using the *GLIM* macro *kfit.mac* (Crawley 1993). This macro also estimates the NB parameter k , which can be applied as a constant in GLMs with a NB error term, e.g. *ownnb.mac* (Crawley 1993), a macro using the *own* directive in *GLIM*. The goodness-of-fit of the NB was estimated through the log-likelihood ratio test observator G (Crawley 1993):

$$G = 2 \sum_{i=1}^a f_i \ln \frac{f_i}{\hat{f}_i},$$

where f_i are the observed and \hat{f}_i the expected frequencies. G is approximately χ^2 distributed with $a-1$ degrees of freedom, where a is the number of frequencies greater than 5.

The frequency of occurrence of the species was analysed using the logit link function (so that $0 \leq \mu \leq 1$) and a binomial (presence-absence) error term in the GLMs. Ideally, in binomial (and Poisson) models the residual deviance² should be roughly equal to the residual degrees of freedom. Ratios larger than 2 indicate substantial overdispersion, but may be adjusted for by setting the error variance (the 'scale parameter' in *GLIM*) of the model equal to the ratio between the scaled deviance and the residual degrees of freedom (Pearson's χ^2 , Aitkin *et al.* 1989).

Analysis by GLM was based on the statistical techniques of (i) analysis-of-variance (ANOVA), to test for differences in response (catch rate, frequency-of-occurrence or abundance) between levels of one or more explanatory variables (factors) on a nominal scale, and (ii) linear regression, to test for correlation between the response variable and one or more explanatory variables (factors) on an ordinal or a continuous scale (see Dobson 1990, p. 3). Factors were fitted to the models using the *forward selection procedure* (Draper & Smith 1966, Nichols 1989). F -tests were here used to assess the significance of the change in deviance caused by adding a factor to or deleting it from the model. The significance of the pair-wise dif-

² *Deviance* is a measure of discrepancy, equal to the logarithm of the ratio of two likelihoods, used by *GLIM* to assess the goodness-of-fit of the model to the data.






ferences between factor levels in each (minimum adequate) model was assessed by taking the Student's *t*-ratio between each model parameter estimate and its standard error. Differences between significant levels were further assessed using the *standard error of the difference between two means* (Crawley 1993). Residuals and outliers were checked using informal tests. If not stated otherwise a 5% significance level ($\alpha = 0.05$) was used for all models.

The negative binomial shape parameter *k* is often interpreted as an ecological indicator of the degree of clumping or aggregation in animal populations (Southwood 1966, White & Bennetts 1996). Animal aggregation may be active or due to some heterogeneity factor in the environment (Southwood 1966). Arbous & Kerrich's (1951) formula:

$$\lambda = \frac{\mu}{2k} v,$$

where *v* is a χ^2 distributed function with $2k$ degrees of freedom, gives the mean size λ of an aggregation at a probability level of $v = 0.5$. $\lambda < 2$ is taken to indicate that clumping may be caused by environmental factors, while $\lambda > 2$ would suggest that either factor may be the cause (see Southwood 1966).

Apart from *GLIM* several other programs were also used for statistical (and graphical) analysis:

	Excel v. 4.0	Microsoft Corp. (MacOS/WinOS)
	JMP v. 2.0	SAS Institute (MacOS)
	STATISTICA v. 4.1	StatSoft (MacOS/WinOS)
	DeltaGraph Pro v. 2.0.2	Claris (MacOS)
	MacDraw Pro v. 1.1	Claris (MacOS)

3 RESULTS

3.1 Catch composition

A total of 5438 goldsinny, rock cook and corkwing were caught on 299 beach seine and 360 net sampling stations from July 1986 to August 1990.

3.1.1 Length-frequency distributions

Length measurements on 72% of the beach seine individuals and 81% of the net individuals (Table 4) showed that the nets were highly size-selective compared to the beach seine, resulting for goldsinny and rock cook in particular in typically narrower and more peaked length-frequency curves (Figure 4). The nets held individuals of all the species up to their recorded maximum lengths (see Table 1), but did not catch any fish smaller than 8 to 10 cm. In contrast, the beach seine caught fish over the whole size range; however, the majority of these individuals (81 to 94%) were less than 10 cm in length. Furthermore, a large proportion of rock cook and corkwing in the beach seine samples consisted of mostly young-of-the-year less than 5 cm (66 and 84%, respectively). Goldsinnies in these samples

Table 4 - Size composition of samples of the study species.

Gear type	Species	Total no. caught	Total no. measured (%)	Size range (cm)	Mean size (cm)	SD
Beach seine	Goldsinny	947	745 (79)	1.5 - 19.5	7.3	3.49
	Rock cook	364	224 (62)	1.0 - 15.5	5.2	3.32
	Corkwing	398	254 (64)	1.5 - 23.0	4.2	3.23
Gillnet	Goldsinny	908	753 (83)	8.0 - 17.0	13.3	0.99
	Rock cook	1545	1218 (79)	11.0 - 19.0	13.3	1.35
	Corkwing	428	305 (71)	11.0 - 20.0	13.3	1.59
Trammel-net	Goldsinny	60	60 (100)	10.0 - 17.0	13.7	1.51
	Rock cook	387	339 (88)	12.0 - 20.0	14.7	0.96
	Corkwing	401	354 (88)	12.0 - 24.0	16.2	2.00

Results

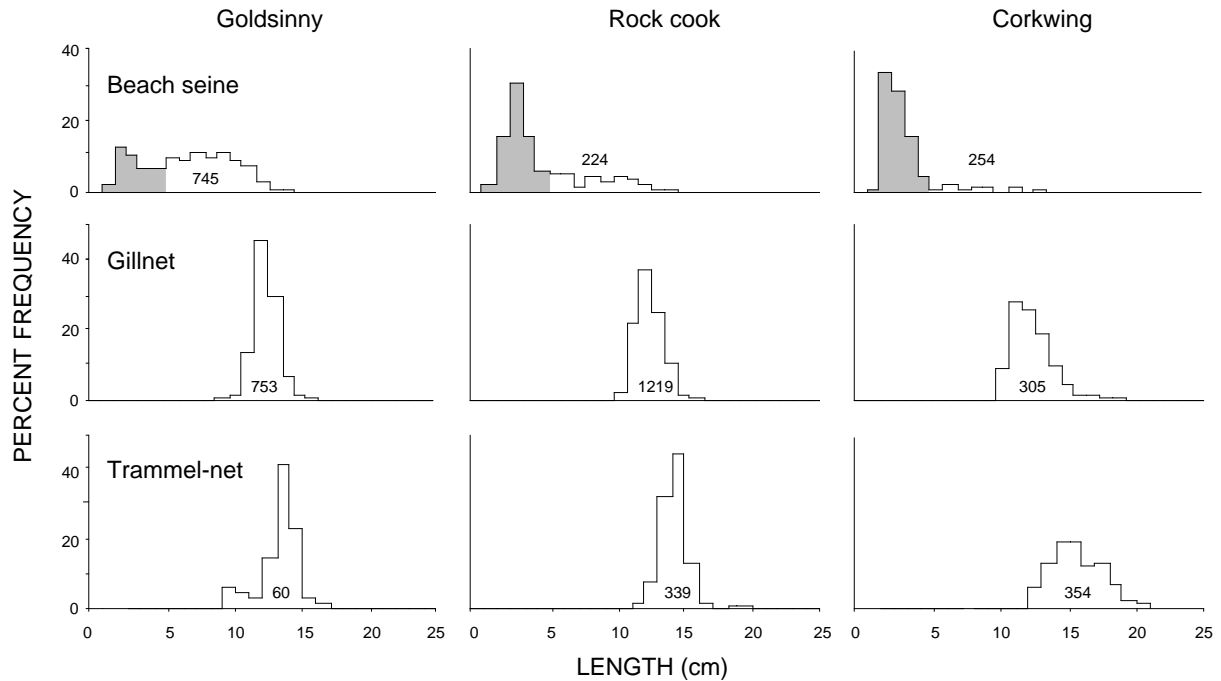


Figure 4 - Size composition of wrasses in the samples. Shaded areas denote the proportion of 0 group individuals (< 5 cm). Numbers refer to the number of individuals that were measured.

were comparatively larger, with only 32% smaller than 5 cm. In the following, juveniles less than 5 cm in the seine samples are referred to as '0 group', larger fish as 'I+ group' (see Table 1 for length-at-age and growth rate estimates).

3.1.2 Catch-frequency distributions

Beach seine

Averaged over all seasons beach seine catch rates were low, with only one to three individuals of a species per haul (Table 5). Overall frequency of occurrence in the samples was also low, with any one species present only in 20 to 44% of the samples. In 51% of the samples none of the species were present.

Goldsinny dominated in the samples (55% of total catch by gear, Table 5), and were about twice as frequent in the samples as the other two species. Catches of rock cook and corkwing consisted chiefly of 0 group juveniles (69.5 and 85.4% of the total catch by species, respectively), whereas for goldsinny the bulk of the catches (64.6%) was made up of one year and older

fish. Frequency of occurrence of goldsinny was about equal for both age groups, whereas rock cook and corkwing were slightly more frequent as 0 group.

Nets

The catch-per-unit-effort from the pooled net samples was overall higher compared to the beach seine (10.4 vs. 5.7 wrasses per sample, respectively). Gillnet catch rates were mostly several times higher than those of the trammel-net, which accounted for only 30.1% of the total net catch (Table 5). Rock cook was by far the most abundant species in the gillnet samples (78.3% of the total catch by gear), whereas goldsinny were somewhat more frequent in these samples. In trammel-net samples goldsinny were, however, greatly under-represented, comprising only 7.1% of the total catch by gear, and occurring in only 7% of the samples. The catchability for corkwing was about equal for both net types, both in terms of sample abundance and frequency of occurrence, but corkwing were on the whole less abundant and frequent in net samples compared to the other two species. In 42% of

Table 5 - Total and mean catch (\pm SD), and frequency of occurrence of wrasses in the samples.

Gear type	Species	Total catch	Mean catch	Standard deviation	Frequency of occurrence
Beach seine	Goldsinny, 0 group	335	1.1	0.16	0.30
	Rock cook, 0 group	253	0.8	0.22	0.14
	Corkwing, 0 group	340	1.1	0.22	0.19
	Goldsinny, I+ group	612	2.0	0.31	0.31
	Rock cook, I+ group	111	0.4	0.10	0.10
	Corkwing, I+ group	58	0.2	0.04	0.12
Gillnet	Goldsinny	908	2.5	0.26	0.47
	Rock cook	1545	4.3	0.51	0.38
	Corkwing	428	1.2	0.20	0.21
Trammel-net	Goldsinny	60	0.2	0.06	0.07
	Rock cook	387	1.1	0.18	0.22
	Corkwing	401	1.1	0.16	0.23

Results

Table 6 - Fit of the negative binomial to the observed catch-frequency distributions. Variance-to-mean ratio of each distribution, estimates of the dispersion parameter k and the clumping parameter λ , the goodness-of-fit statistic G with its associated degrees of freedom (df), and the chi-squared probability value of the G -test (significant p -values are underlined). [...] indicates that the test failed (0 df).

Gear type	Species	Variance - mean ratio	k	λ^\dagger	G	df	$p > \chi^2$
Beach seine	Goldsinny, 0 group	7.1	0.18	0.05	12.42	3	0.01
	Rock cook, 0 group	17.2	0.06	0.01	1.55	0	..
	Corkwing, 0 group	12.5	0.08	0.02	3.57	1	<u>0.06</u>
	Goldsinny, I+ group	14.1	0.14	0.07	10.24	3	0.02
	Rock cook, I+ group	8.4	0.05	0.004	0.46	0	..
	Corkwing, I+ group	2.0	0.16	0.01	2.37	0	..
Nets	Goldsinny	9.9	0.28	0.11	7.46	6	<u>0.28</u>
	Rock cook	26.2	0.16	0.09	13.85	5	0.02
	Corkwing	14.7	0.14	0.03	5.77	4	<u>0.22</u>

\dagger with df = 1

the net samples none of the species were present.

The catch-frequency distributions of the study species (Table 6) generally had high variance-to-mean ratios (2-26), suggesting a good approximation by the negative binomial (Southwood 1966). The goodness-of-fit of the negative binomial was assessed by G -tests, which showed that the smallest catch distributions - net catches of goldsinny and net and seine catches of corkwing - fitted the theoretical distribution well ($p\chi^2 > 0.05$, Table 6). For the other frequency distributions the G -tests either gave no significant results, presumably because larger catch distributions are generally more skewed (M. Pennington, pers. comm.), or failed, because not enough comparisons could be made (given that each frequency should be greater than or equal to 5, so that the degrees of freedom exceed zero). The dispersion parameter k - which is valid regardless of the result of the G -test (M. Pennington, pers. comm.) - was always much less than 1 (Table 6), indicating that all of the distributions are highly aggregated. The high variances, low means and small k values together suggest that the negative bi-

nomial for practical purposes provides a close enough approximation to all of the observed catch-frequency distributions. A negative binomial error term was therefore assumed in all subsequent models of wrasse catch rates.

Although the degrees of freedom of the clumping parameter λ (as defined by $2k$) were always less than one, assuming one degree of freedom for the parameter estimation still gave a tendency of λ toward zero (Table 6) for all catch distributions. Such low estimates of the clumping parameter would indicate, as suggested in Southwood (1966), that aggregations of the study species are caused by environmental factors rather than by active behaviour of the species themselves.

3.2 Temporal effects

The activity of the wrasses, and consequently their availability to capture, was highly cyclical throughout each year (Figure 5). Numbers in the catches were generally low during the first quarter, started to rise in May, and peaked during the third quarter. From September on catch rates started to decline again, approaching low to zero levels in December/January.

Tables 7 and 8 show the mean catch in numbers of fish per quarter and per year, respectively, as well as the effect of the factors *quarter* and *year* on catch rates. This effect is shown relative to a factor level whose parameter estimate was *aliased* (i.e. set to zero in the model, as a rule level 1).

3.2.1 Seasonal variation in abundance

It can be seen from Figure 5 that the catch rates varied greatly between quarters, as indicated by the model *F*-ratios (Table 7) which were highly significant for all species, especially in the net fishery ($p < 0.001$ for all models).

Catch rates were invariably highest during the 3rd quarter, although not always significantly higher than during the preceding quarter. During the 1st quarter in particular, the wrasses were generally absent from or only

Results

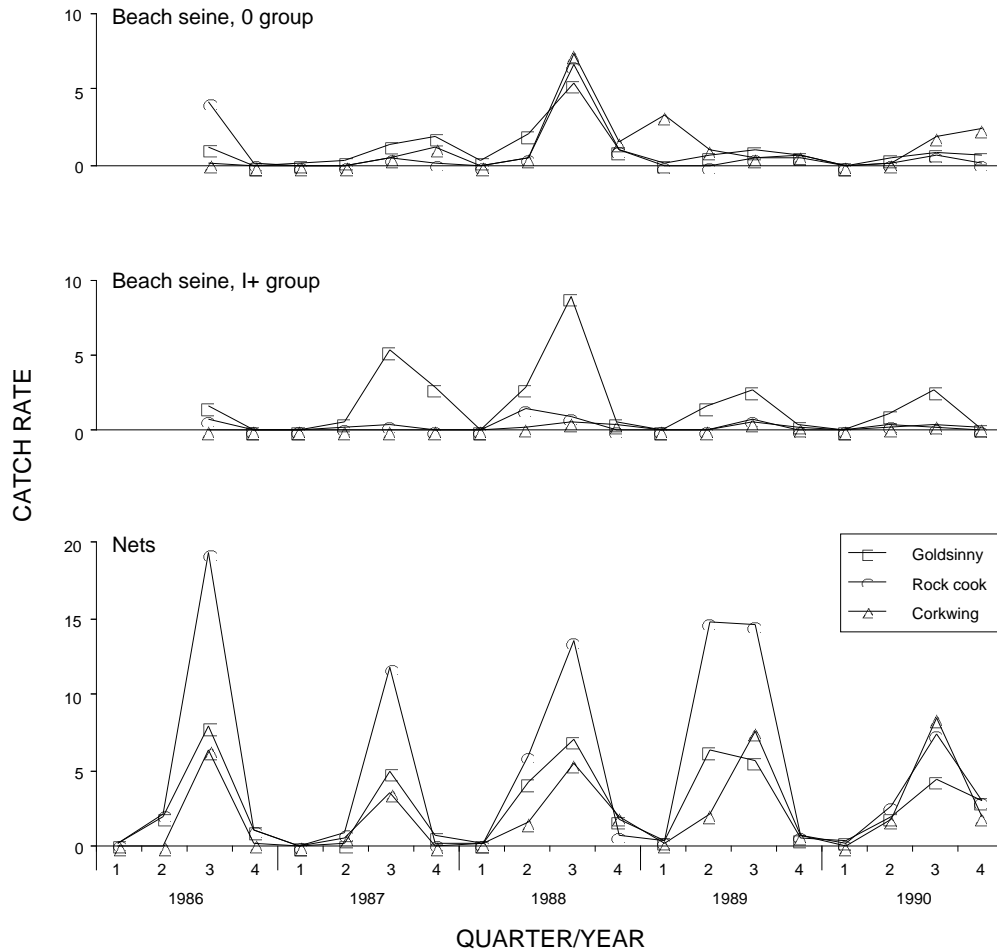


Figure 5 - Mean catch of the study species for each quarter of each year.

present in small numbers in the samples. In contrast, catch rates of 0 group corkwing were significantly higher during the 1st quarter than during the 2nd, but not different from catch rates during the rest of the year. This effect was largely due to high abundance in samples from February 1989 on sites no. 16 and 17 (subarea 2).

3.2.2 Annual variation in abundance

Catch rates varied less between than within years (Figure 5), but the effect of the factor year was still largely significant. This effect was greatest for beach seine catch rates ($p \leq 0.01$, Table 8), largely due to a

Table 7 - Seasonal differences in wrasse catch rates. Mean catch per quarter of the year, maximum likelihood \log_e estimates and standard errors (SE) of model parameters (quarters) relative to aliased parameters, and estimates (\pm SE) of differences between significant parameters. Significant model parameters and F -ratios are underlined.

Model parameter	Goldsinny			Rock cook			Corkwing		
	Mean	Estimate	SE	Mean	Estimate	SE	Mean	Estimate	SE
Beach seine, 0 group									
Intercept		-1.79	0.47		-1.77	0.26		0.06	0.42
Quarter 1	0.17	0		0.00	0		1.07	0	
Quarter 2	0.95	<u>1.74</u>	0.51	0.17	0		0.27	<u>-1.37</u>	0.49
Quarter 3	2.03	<u>2.5</u>	0.51	2.28	<u>2.6</u>	0.35	2.3	0.77	0.49
Quarter 4	0.68	<u>1.4</u>	0.52	0.41	<u>0.89</u>	0.37	0.95	<u>-0.12</u>	0.5
Qtr 2-3		<u>-0.76</u>	0.28						
Qtr 2-4		0.34	0.3						
Qtr 3-4		<u>1.1</u>	0.3		<u>1.71</u>	0.35			
F -ratio	<u>9.95</u>			<u>28.7</u>			<u>11.71</u>		

Beach seine, I+ group									
Intercept		0.43	0.21		-0.53	0.22		-3.4	0.63
Quarter 1	0.0	0		0.0	0		0.03	0	
Quarter 2	1.53	0		0.59	0		0.13	<u>1.36</u>	0.66
Quarter 3	4.6	<u>1.1</u>	0.31	0.56	-0.05	0.32	0.37	<u>2.41</u>	0.65
Quarter 4	0.63	<u>-0.9</u>	0.33	0.03	<u>-3.16</u>	0.45	0.14	<u>1.42</u>	0.67
Qtr 2-3								<u>-1.05</u>	0.28
Qtr 2-4								-0.06	0.32
Qtr 3-4		<u>2.0</u>	0.31					<u>0.99</u>	0.3
F -ratio	<u>17.97</u>			<u>26.6</u>			<u>9.74</u>		

Nets									
Intercept		-1.69	0.21		-1.85	0.23		-2.66	0.28
Quarter 1	0.18	0		0.16	0		0.07	0	
Quarter 2	2.67	<u>2.67</u>	0.28	4.7	<u>3.39</u>	0.31	0.96	<u>2.62</u>	0.35
Quarter 3	5.93	<u>3.47</u>	0.25	13.25	<u>4.43</u>	0.29	6.11	<u>4.47</u>	0.33
Quarter 4	1.21	<u>1.89</u>	0.3	0.82	<u>1.65</u>	0.35	0.93	<u>2.58</u>	0.38
Qtr 2-3		<u>-0.8</u>	0.22		<u>-1.04</u>	0.26		<u>-1.85</u>	0.27
Qtr 2-4		<u>0.79</u>	0.28		<u>1.74</u>	0.33		0.03	0.33
Qtr 3-4		<u>1.59</u>	0.26		<u>2.78</u>	0.31		<u>1.88</u>	0.3
F -ratio	<u>65.07</u>			<u>78.39</u>			<u>71.34</u>		

Results

Table 8 - Differences in wrasse catch rates between years. Maximum likelihood \log_e estimates and standard errors (SE) of model parameters (years) relative to aliased parameters, and estimates (\pm SE) of differences between significant parameters. Significant model parameters and F -ratios are underlined.

Model parameter	Goldsinny			Rock cook			Corkwing		
	Mean	Estimate	SE	Mean	Estimate	SE	Mean	Estimate	SE
Beach seine, 0 group									
Intercept		-1.06	0.41		0.27	0.43		-1.25	0.31
1986	0.34	0		1.31	0		0.03		
1987	0.81	0.85	0.47	0.14	<u>-2.22</u>	0.53	0.29	0	
1988	2.42	<u>1.95</u>	0.46	2.11	0.48	0.5	2.4	<u>2.13</u>	0.4
1989	0.65	0.63	0.48	0.32	<u>-1.42</u>	0.53	1.03	<u>1.29</u>	0.43
1990	0.58	0.52	0.49	0.28	<u>-1.53</u>	0.53	1.08	<u>1.33</u>	0.43
87-88					0.8	0.45			
87-89					0.68	0.45			
88-89								<u>0.84</u>	0.39
88-90								<u>0.8</u>	0.38
89-90					-0.11	0.45		<u>-0.05</u>	0.42
F -ratio	<u>7.8</u>			<u>14.53</u>			<u>8.55</u>		

Beach seine, I+ group									
Intercept		-0.59	0.44		-1.42	0.45		-1.25	0.22
1986	0.55	0		0.24	0		0.0		
1987	2.23	<u>1.39</u>	0.51	0.19	-0.26	0.54	0.03		
1988	3.41	<u>1.81</u>	0.5	0.79	<u>1.18</u>	0.52	0.29	0	
1989	1.3	0.85	0.53	0.28	0.16	0.55	<u>0.28</u>	-0.01	0.34
1990	1.48	0.98	0.53	0.18	-0.27	0.55	<u>0.27</u>	-0.08	0.34
87-88		-0.42	0.36						
F -ratio	<u>3.78</u>			<u>5.36</u>			<u>11.38</u>		

Nets									
Intercept		1.02	0.22		1.75	0.27		0.48	0.27
1986	2.78	0		5.74	0		1.61	0	
1987	1.69	-0.49	0.3	4.01	-0.36	0.37	1.28	-0.23	0.37
1988	3.31	0.18	0.3	5.31	-0.08	0.37	2.36	0.38	0.36
1989	3.15	0.13	0.31	7.62	0.29	0.38	3.08	0.65	0.38
1990	2.48	-0.11	0.36	3.75	-0.42	0.44	4.0	<u>0.91</u>	0.43
F -ratio	1.54			1.01			<u>2.72</u>		

marked 1988 peak in abundance which could be observed for both age groups of all three species. Net catch rates did not differ between years, except for a slight tendency of increasing corkwing abundance throughout the study period, peaking significantly in 1990 compared to other years ($p < 0.05$).

3.3 Spatial effects

Figures 6-8 and 10-12 show the frequency of occurrence and catch abundance (excluding zero catch) of the study species in winter and summer samples from each subarea (Figures 6-8) and from each habitat (Figures 10-12). The plots on the right-hand side show parameter estimates of significant terms in the models (the terms are *season*, *subarea* or *habitat*, *season * subarea* or *season * habitat* interaction), with error bars indicating the 95% confidence limits of each parameter estimate. Frequency of occurrence was modelled using a binomial error term; for the catch abundances a Poisson error term for counts was assumed, with Pearson's χ^2 adjustment for overdispersion. Modelling was otherwise done as in the previous section.

3.3.1 Association with subarea

Spatial association in goldsinny shifted from outer area for 0 group through central area for I+ group to central/inner subarea for net-caught fish. For rock cook a spatial association with subarea was on the whole not apparent, while corkwing occurrence and abundance increased consistently from the inner to the outer fjord area. A seasonal (summer) effect was evident on I+ group levels of occurrence, and on the distribution of net-caught individuals in particular. No seasonal interaction effects with area were found.

Beach seine, 0 group (Figure 6)

The frequency of occurrence of juvenile goldsinny in the samples increased from inner to outer fjord area; the presence of corkwing showed a similar tendency, with a significantly higher frequency and slightly higher abundance in samples from the outermost subarea compared to the fjord proper. No significant effects were found on rock cook occurrence, but the abun

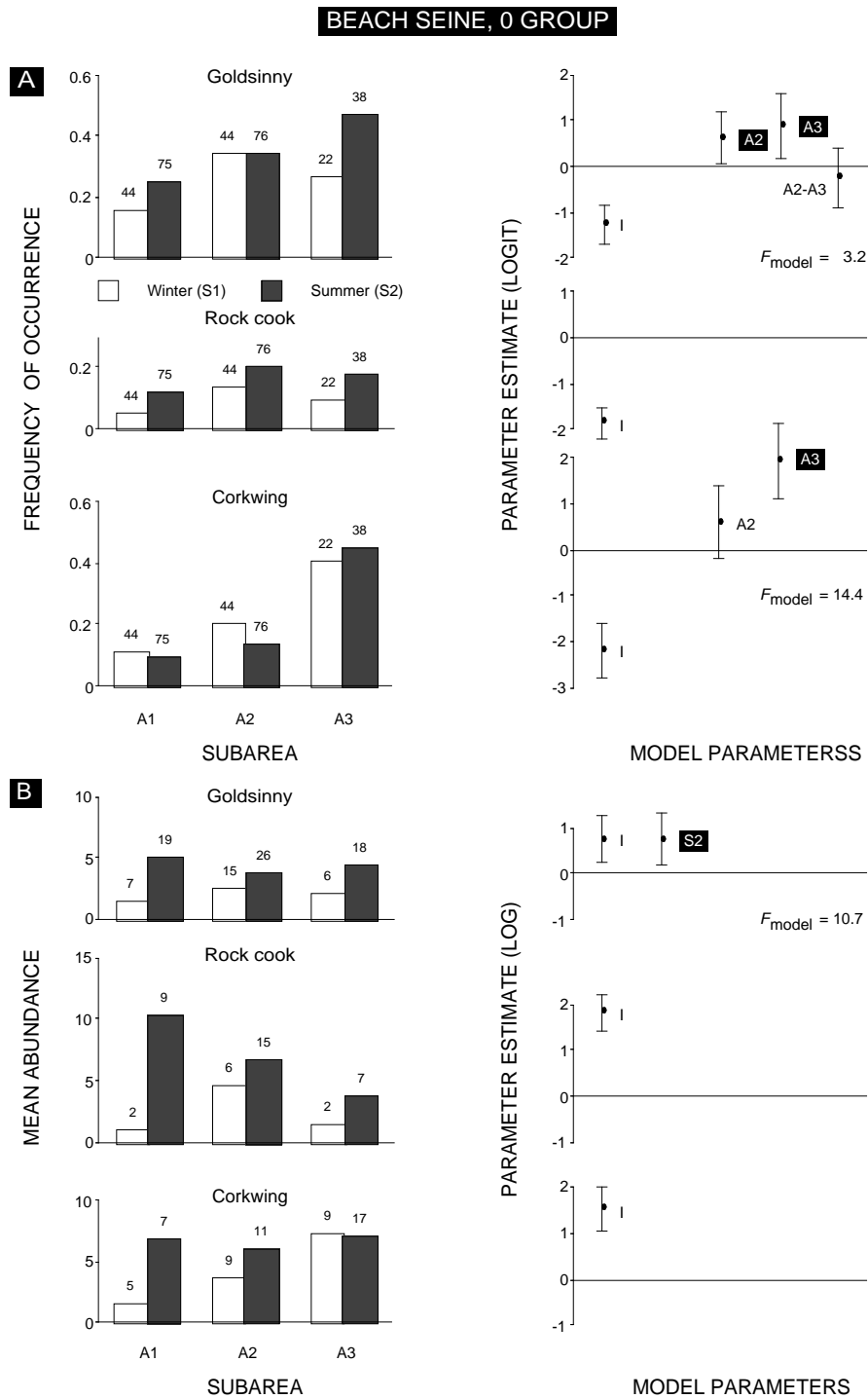


Figure 6 - Effect of subarea (A1-3) and season (S1-2) on (A) the frequency of occurrence and (B) the mean abundance (zero catch excluded) of 0 group wrasses in the beach seine samples. Right hand plots show maximum likelihood logit (A) and \log_e estimates (B) and 95% confidence intervals of significant model terms and parameters (1 = intercept). Significant parameters at the $\alpha = 0.05$ level are outlined.

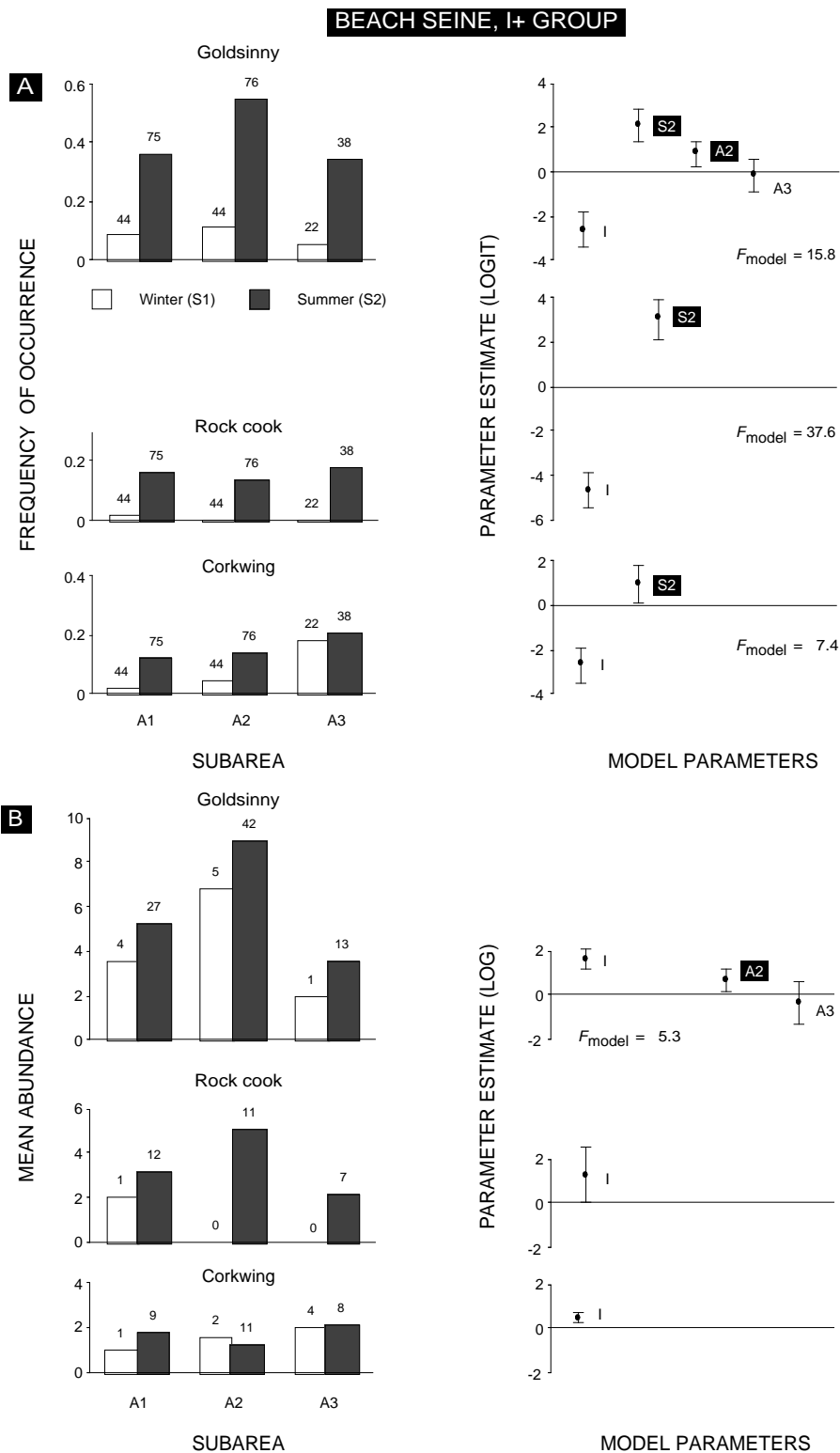


Figure 7 - Effect of subarea (A1-3) and season (S1-2) on (A) the frequency of occurrence and (B) the mean abundance (zero catch excluded) of I+ wrasses in the beach seine samples. Right hand plots show maximum likelihood logit (A) and \log_e estimates (B) and 95% confidence intervals of significant model terms and parameters (I = intercept). Significant parameters at the $\alpha = 0.05$ level are outlined.

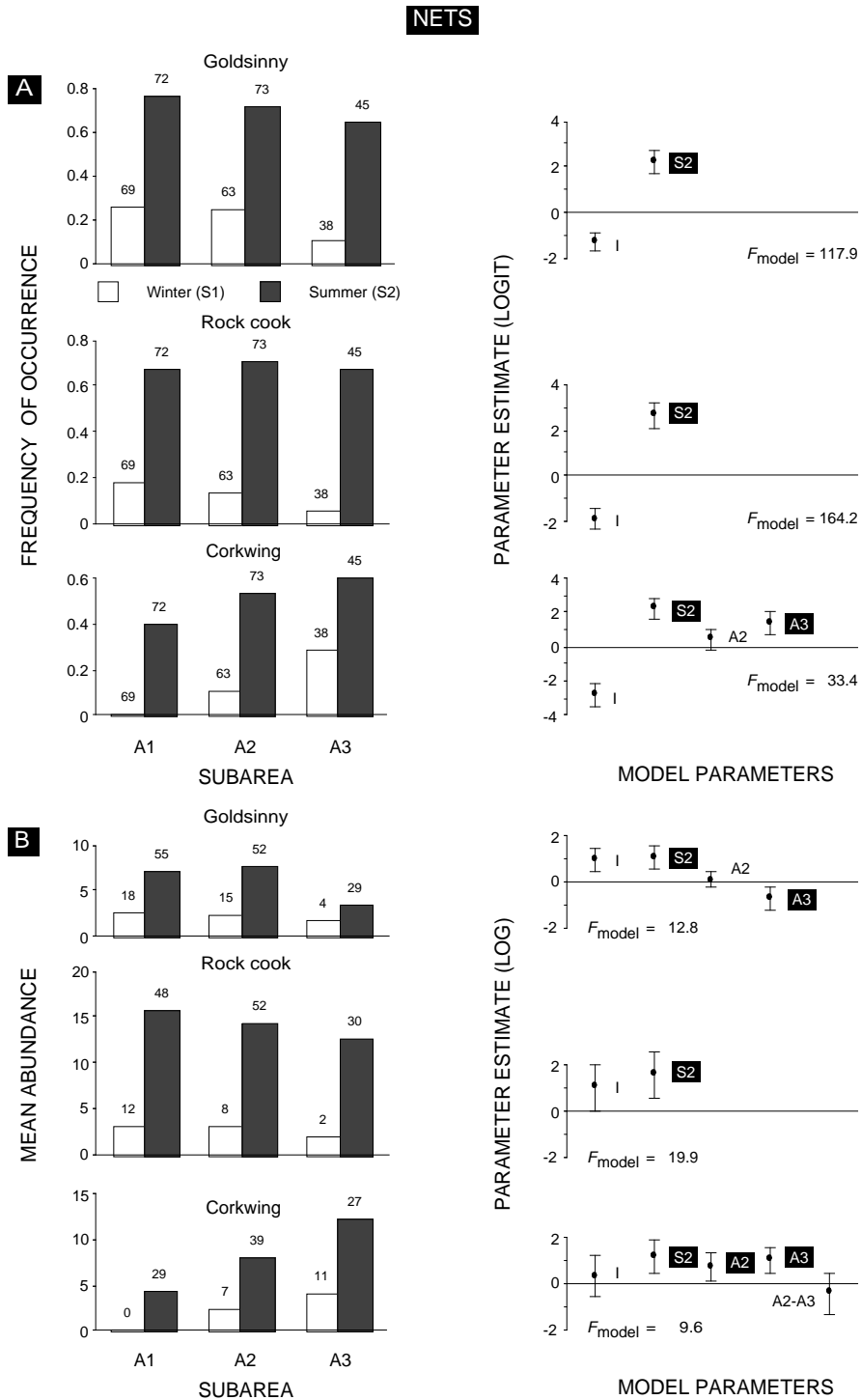


Figure 8 - Effect of subarea (A1-3) and season (S1-2) on (A) the frequency of occurrence and (B) the mean abundance (zero catch excluded) of wrasses in the net samples. Right hand plots show maximum likelihood logit (A) and \log_e estimates (B) and 95% confidence intervals of significant model terms and parameters (1 = intercept). Significant parameters at the $\alpha = 0.05$ level are outlined.

dance of this species in summer samples appeared to be slightly greater towards the inner parts of the fjord.

Beach seine, I+ group (Figure 7)

Significantly higher presence and abundance levels were found in the central subarea for I+ group goldsinny compared to outer fjord area for 0 group. Rock cook were almost absent from winter samples, and in summer samples appeared to be evenly distributed over the whole study area. Corkwing were somewhat more frequently caught during the summer season, and also appeared increasingly frequent and abundant towards the outer fjord areas.

Net samples (Figure 8)

Goldsinny wrasses in the net samples were significantly less abundant in summer samples from the outermost area compared to the fjord proper; there was a similar, but non-significant effect on goldsinny occurrence. Rock cook appeared to be evenly distributed over the whole study area for these samples as well. Corkwing showed a clear and significant tendency of increasing occurrence and abundance from inner to outer fjord area.

3.3.2 Association with habitat

Weighted group-average cluster analysis (Digby & Kempton 1987) performed on a matrix of similarities between the study sites (Appendix 7) suggested grouping the study sites into three broad habitat types at about 42% dissimilarity (Figure 9). Within the first cluster two smaller habitat groups were defined at a slightly higher level of similarity (note: since one of the groups contained only one beach seine sampling site, the two groups were combined for the beach seine analysis):

ia) 'Sheltered rocky shore'. Moderately steep rocky littoral, mostly covered by groups of wracks like *Ascophyllum* and *Fucus vesiculosus*. Gradually inclining sandy bottom below 5 m, occasionally with patches of *L. saccharina*.

Results

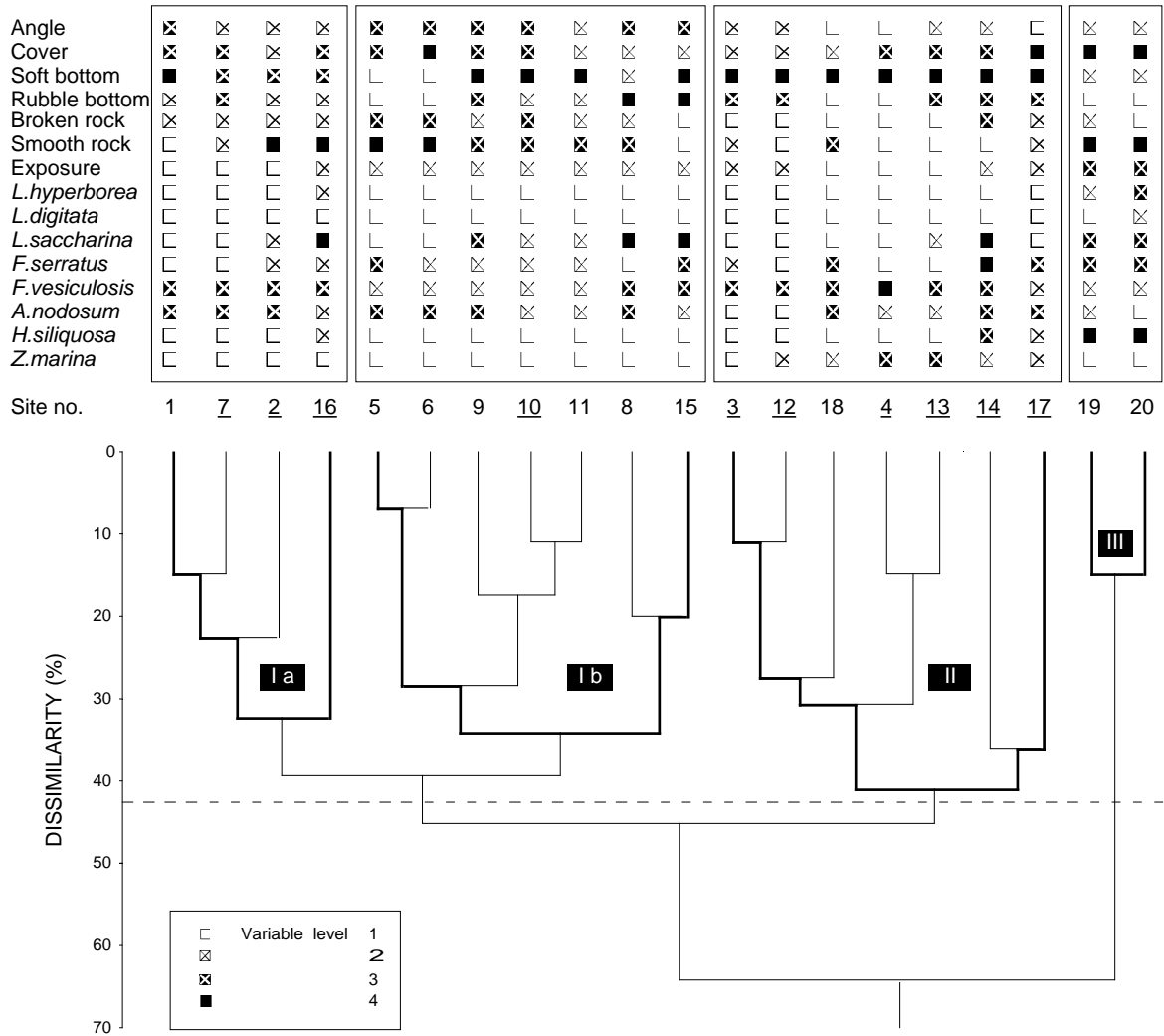


Figure 9 - Matrix of habitat variable levels (including exposure and macrophytes) for each study site, and tree diagram showing sites grouped by four habitat types, generated by cluster analysis on a matrix of similarities between the study sites. The dashed line indicates the percentage dissimilarity at which the clusters were identified. Beach seine sampling sites are underlined.

ib) 'Exposed rocky shore'. Steep and exposed littoral consisting chiefly of bedrock and/or broken rock, with a moderate to high degree of cover of *Ascophyllum*, *F. vesiculosus* and *F. serratus*. Below 5 m the substratum is sandy or muddy, often with *L. saccharina*.

ii) 'Mudflats'. Shallow, sheltered locations in bays or enclosed between islets. *Ascophyllum*/*F. vesiculosus* cover most of the sandy and/or grainy littoral. Further out from the shore the substratum is muddy, with frequent tufts of *Zostera*.

iii) 'Kelp forest'. Outer localities, highly exposed to wind and waves, with a substratum consisting of bedrock/broken rock partly covered by sand or mud. Large kelps like *L. hyperborea* dominate. This habitat was only sampled by nets.

For the net samples, occurrence as well as abundance of goldsinny and rock cook was significantly lower on mudflat compared to rocky shore habitat, particularly during winter (Figure 10). Beach seine samples, on the other hand, showed no significant differential association with either habitat for any of the species (Figure 11 and 12). However, goldsinny and I+ rock cook appeared to be slightly more often found over rocky shore habitat, whereas corkwing and 0 group rock cook appeared to be somewhat more associated with mudflats. None of the species were present in net samples from kelp forest habitat in winter, but the frequency of occurrence on this habitat was slightly higher in summer samples. No effect of habitat was evident on net samples of corkwing. Seasonal interaction effects with habitat were not found.

NETS

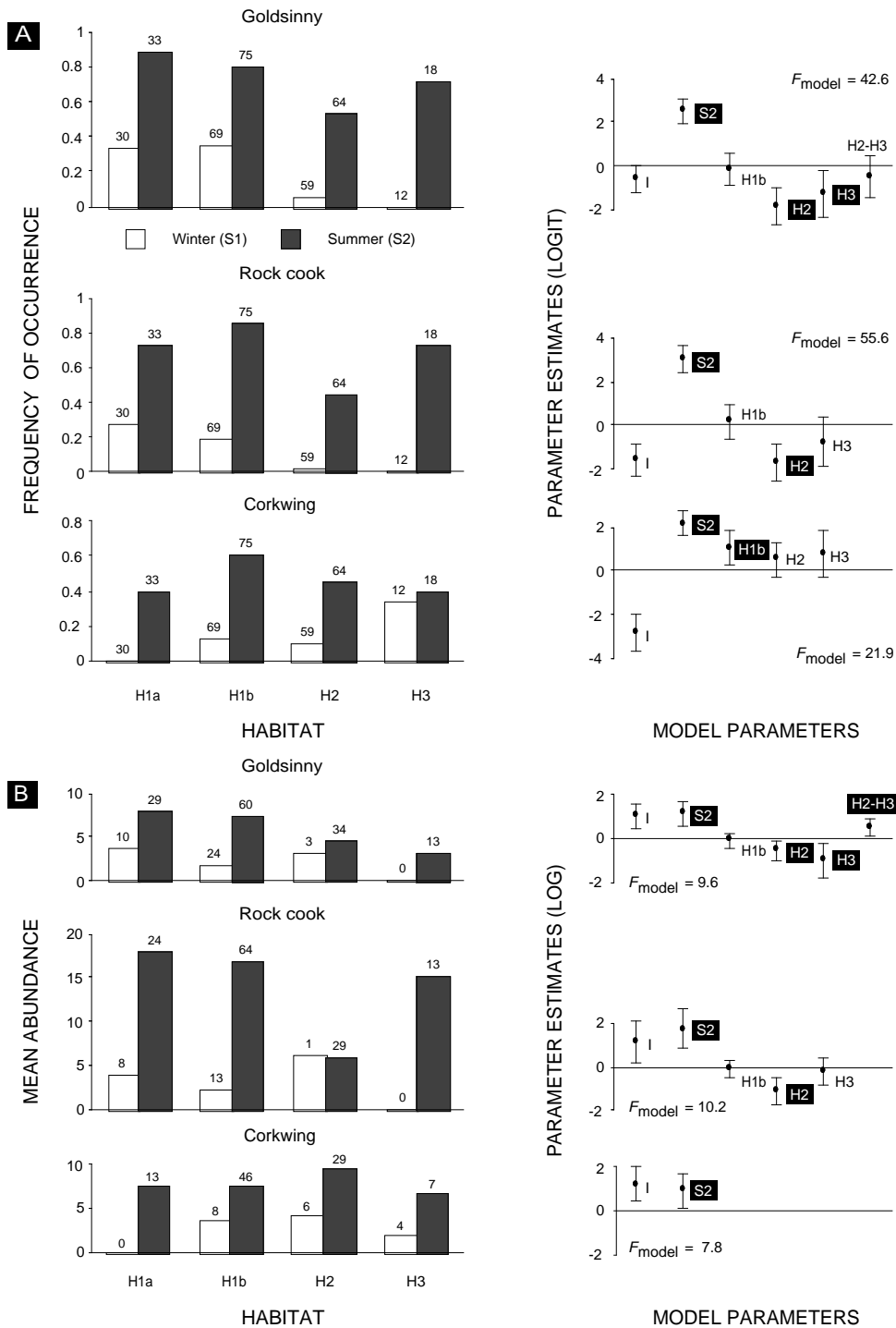


Figure 10 - Effect of *habitat* (H1-2) and *season* (S1-2) on (A) the frequency of occurrence and (B) the mean abundance (zero catch excluded) of wrasses in the net samples. Right hand plots show maximum likelihood logit (A) and \log_e estimates (B) and 95% confidence intervals of significant model terms and parameters (1 = intercept), and the F -value associated with each model. Significant parameters at the $\alpha = 0.05$ level are outlined. Numbers above the bars refer to the number of samples.

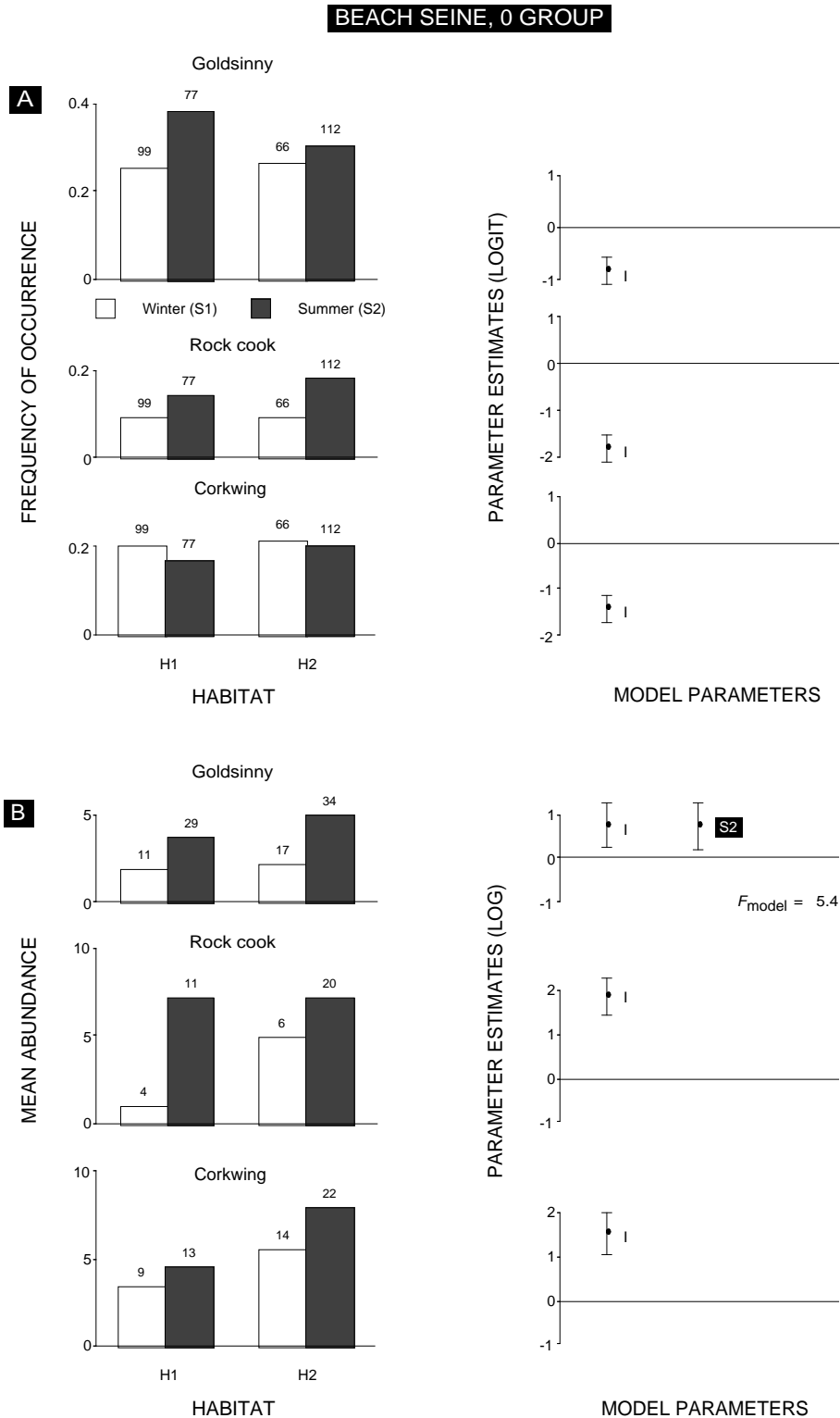


Figure 11 - Effect of *habitat* (H1-2) and *season* (S1-2) on (A) the frequency of occurrence and (B) the mean abundance (zero catch excluded) of 0 group wrasses in the beach seine samples. Right hand plots show maximum likelihood logit (A) and \log_e estimates (B) and 95% confidence intervals of significant model terms and parameters (1 = intercept), and the F -value associated with each model. Significant parameters at the $\alpha = 0.05$ level are out-lined. Numbers above the bars refer to the number of samples.

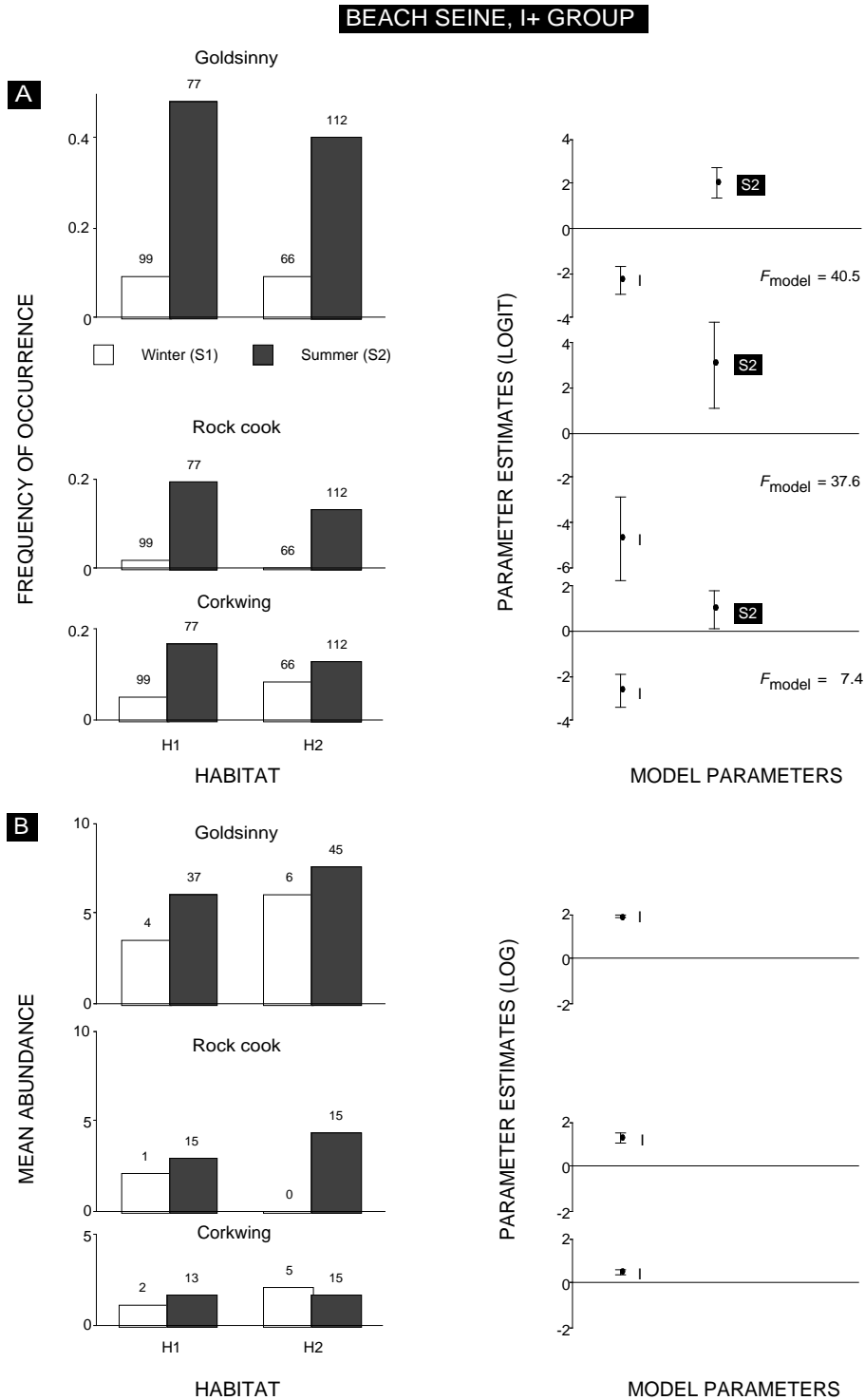


Figure 12 - Effect of *habitat* (H1-2) and *season* (S1-2) on (A) the frequency of occurrence and (B) the mean abundance (zero catch excluded) of I+ wrasses in the beach seine samples. Right hand plots show maximum likelihood logit (A) and \log_e estimates (B) and 95% confidence intervals of significant model terms and parameters (1 = intercept), and the F -value associated with each model. Significant parameters at the $\alpha = 0.05$ level are outlined. Numbers above the bars refer to the number of samples.

3.4 Environmental effects

3.4.1 Effects of habitat-related variables

Habitat-related variables were fitted as ordinal covariates to regression models of catch rates in order to assess which variables were most important in explaining wrasse abundance. Only the main effect of each variable was considered, and whether it interacted with season. The degree of algal cover was not considered as a factor in the net models, because the nets mostly fished below the densest parts of the algal belt. Figure 13 shows scatter plots and frequency distributions of habitat-related variable levels, and correlation coefficients between each variable based on Spearman rank order correlation for ordinal variables (Sokal & Rohlf 1995). The variables generally only showed weak correlation. There was a significant, positive association between substratum angle and broken rock ($r = 0.47$, $p = 0.04$), while soft and rubble substrata were both negatively associated with smooth rock ($r = -0.76$ with $p < 0.01$ and $r = -0.56$ with $p = 0.01$, respectively).

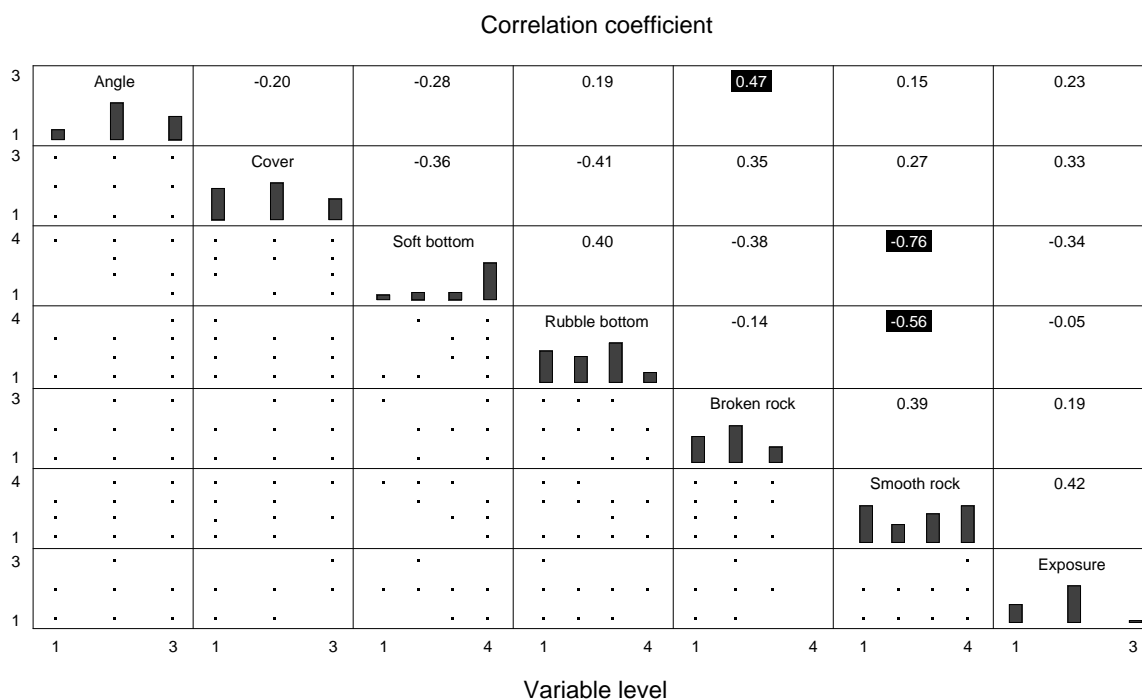


Figure 13 - Matrix showing frequency distributions of levels of habitat-related variables (diagonal), pairwise scatterplots of variable levels (bottom left), and Spearman rank order correlation coefficients r between each variable (top right). Outlined coefficients are significant at the $\alpha = 0.05$ level.

Results

Figures 14-16 show catch rates for each level of each variable and the F -ratio associated with adding it as a factor to a model. Results of the forward selection (see section 2.8) of significant factors to retain in the models are shown in Table 9 for the beach seine samples and in Table 10 for the net samples.

Beach seine samples

Catch rates of goldsinny and rock cook appeared to be mostly affected by increasing coarseness of the substratum, whereas increasing cover availability appeared to be the most important factor explaining catch rates of corkwing (Figures 14-15, Table 9). Juveniles and adults seemed to be associated with basically the same variables. Catches of goldsinny were highest over rubble bottom and broken rock. Rock cook were also positively associated with broken rock, but in addition showed a stronger, negative association with smooth rock and soft bottom. For I+ rock cook steepness and cover also appeared to influence abundance. Corkwing seemed to have no particular preference for any one substratum type, as long as availability of macroalgae was high. The effect of exposure was not significant, except for I+ rock cook, but the general tendency appeared to be that catch rates increased with increasing exposure. Habitat variables tended to explain more of the residual variation in the I+ group models: 19-42%, as compared to only 3-15% for the 0 group models (Table 9), probably because of the additional seasonal influence on I+ abundance.

Net samples

The seasonal influence was stronger on net than on seine individuals (Figure 16), with a number of interaction effects with habitat factors (Table 10). The seasonal effect, as in previous sections, accounted for much of the explained variation in these habitat models. Net catches were for all three species generally explained by increasing rockiness. In models of goldsinny and rock cook abundance this effect is expressed through a correlation with increasing substratum angle and decreasing degree of exposure (see Figure 13).

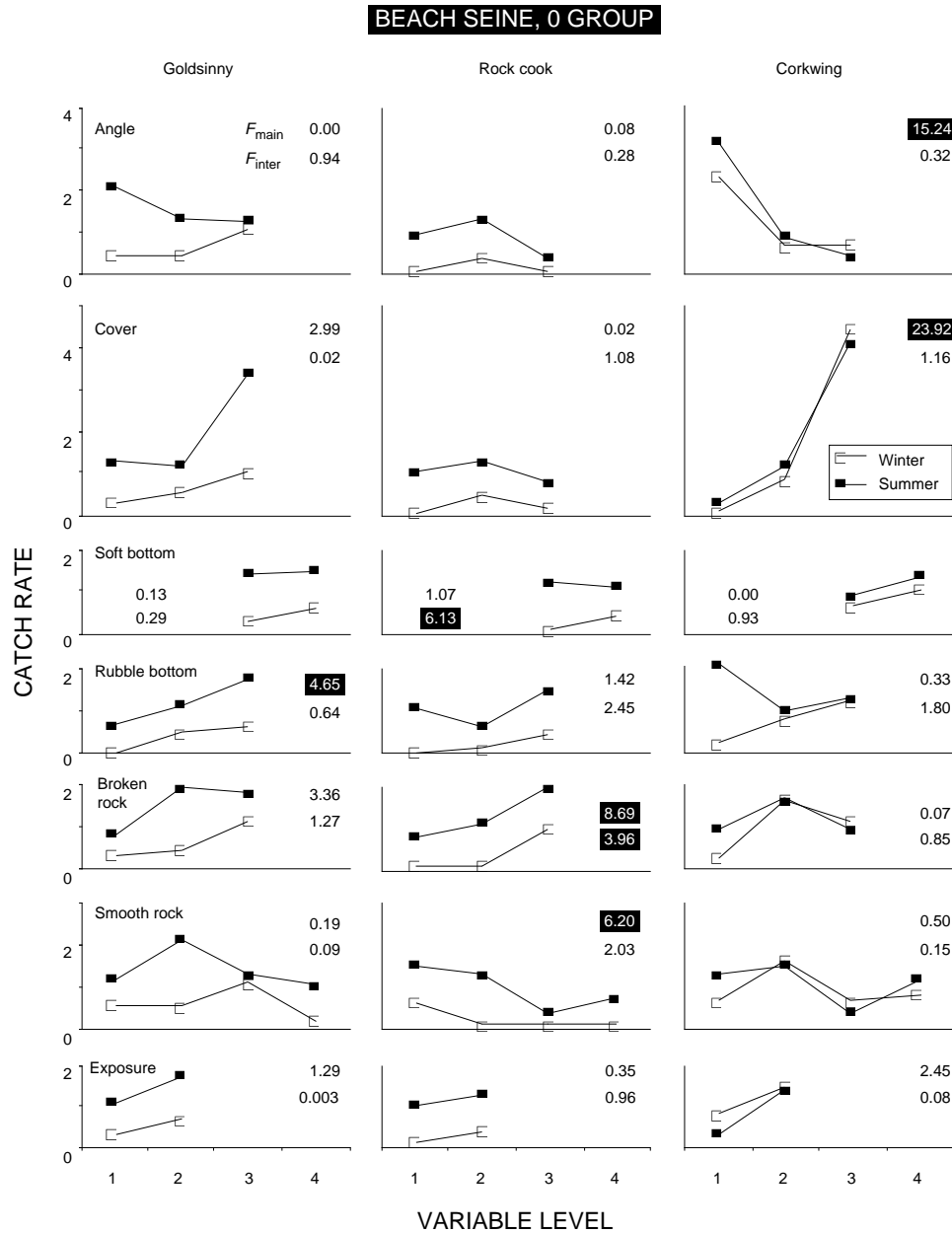


Figure 14 - Mean catch in numbers of 0 group wrasses by beach seine during winter and summer for each of six habitat variable levels (including exposure). Numbers refer to the F -ratios of each factor's main effect (F_{main}) and its interaction with season (F_{inter}). Significant effects at the $\alpha = 0.05$ level are outlined.

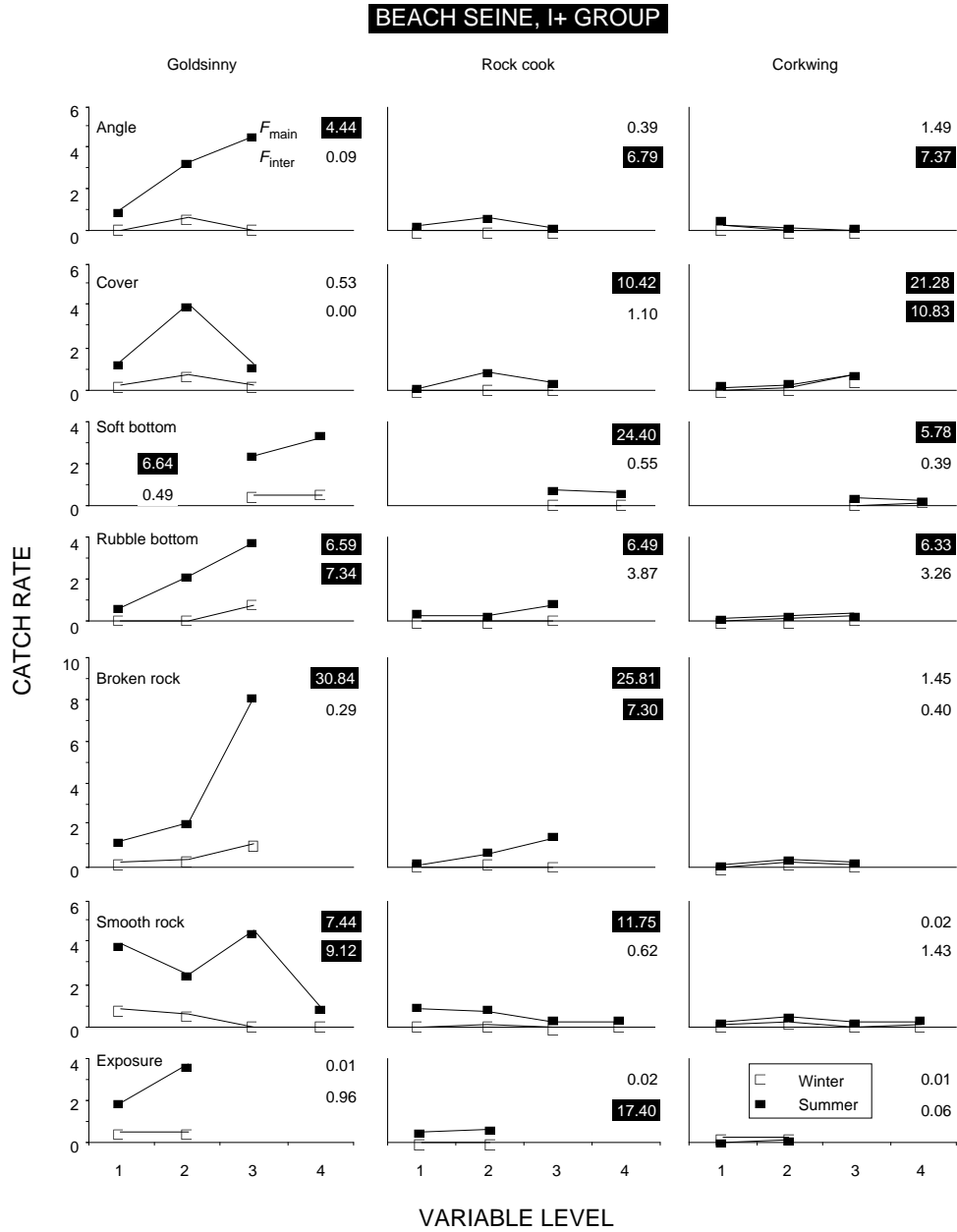


Figure 15 - Mean catch in numbers of I+ group wrasses by beach seine during winter and summer for each of six habitat variable levels (including exposure). Numbers refer to the F -ratios of each factor's main effect (F_{main}) and its interaction with season (F_{inter}). Significant effects at the $\alpha = 0.05$ level are outlined.

Table 9 - Effect of habitat factors on beach seine catch rates of wrasses. Maximum likelihood \log_e parameter estimates and standard errors of model terms, and percentage explained variation (r^2) from each model.

Species	Model term	Parameter estimate	Standard error	Coefficient of determination (r^2)
0 group				
Goldsinny	Intercept	-0.71	0.27	0.03
	Rubble	2.73	0.999	
	Broken rock	1.601	0.71	
Rock cook	Intercept	-1.301	0.71	0.15
	Soft bottom	-4.36	0.93	
	Soft bottom.summer	3.014	0.47	
	Broken rock	1.89	0.91	
	Smooth rock	-2.56	0.72	
Corkwing	Intercept	-2.34	0.52	0.08
	Cover	1.18	0.26	

I+ group				
Goldsinny	Intercept	-6.39	0.93	0.32
	Season	5.71	0.93	
	Rubble	17.92	3.13	
	Rubble.summer	-13.89	3.29	
	Broken rock	4.802	0.74	
Rock cook	Intercept	-10.7	2.66	0.42
	Season	12.35	2.66	
	Angle	0.45	0.12	
	Angle.summer	-0.44	0.12	
	Cover	0.94	0.33	
	Soft bottom	-5.73	0.89	
	Smooth rock	-4.97	0.76	
Corkwing	Intercept	-6.91	1.18	0.19
	Season	5.32	1.29	
	Cover	2.78	0.52	
	Cover.summer	-1.94	0.57	
	Soft bottom	-2.44	0.62	

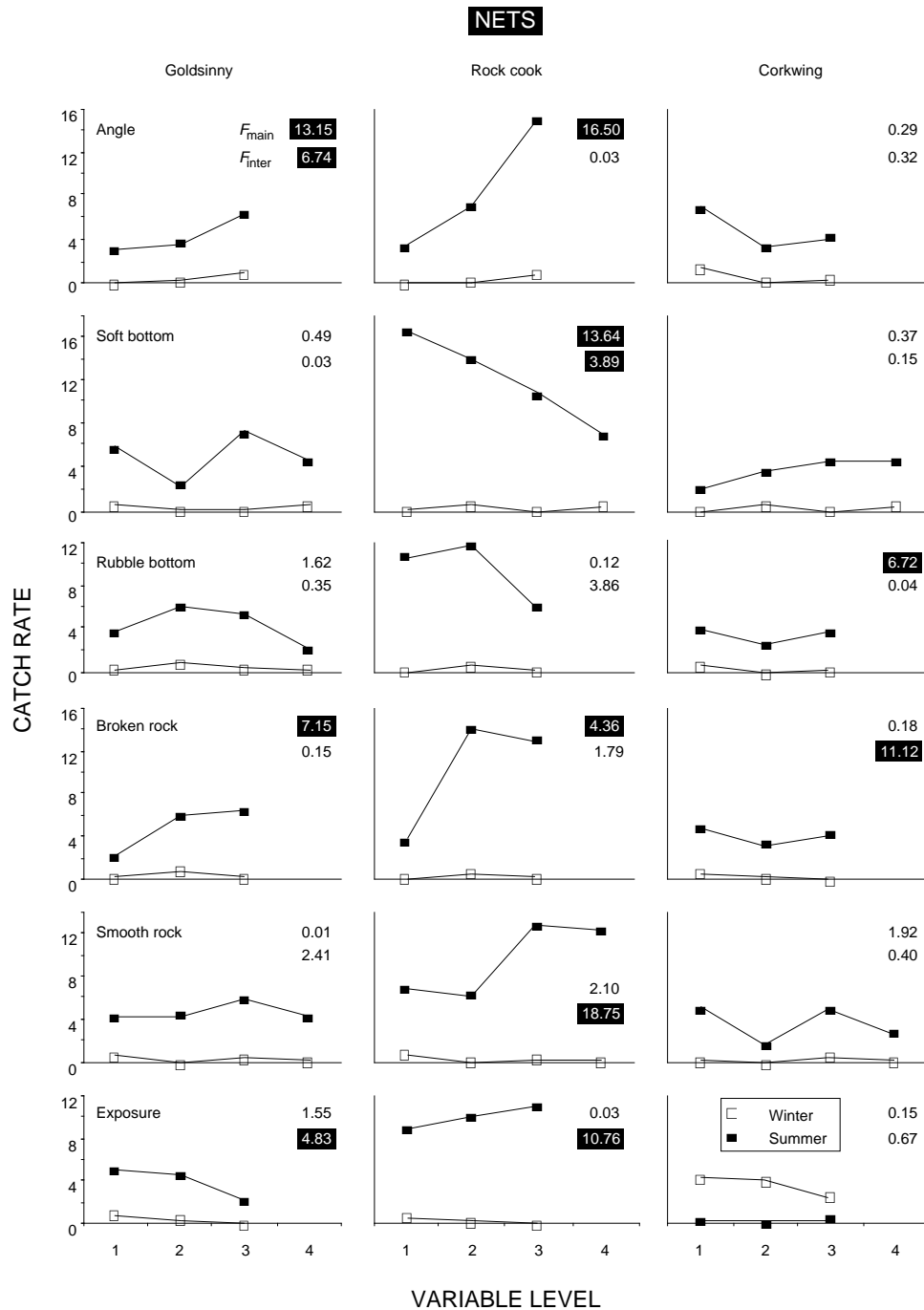


Figure 16 - Mean catch in numbers of wrasse by the nets during winter and summer for each of six habitat variable levels (including exposure). Numbers refer to the F -ratios of each factor's main effect (F_{main}) and its interaction with season (F_{inter}). Significant effects at the $\alpha = 0.05$ level are outlined.

Table 10 - Effect of habitat factors on net catch rates of wrasses. Maximum likelihood \log_e parameter estimates and standard errors of model terms, and percentage explained variation (r^2) from each model.

Species	Model term	Parameter estimate	Standard error	Coefficient of determination (r^2)
Goldsinny	Intercept	-1.71	0.29	0.34
	Season	2.15	0.23	
	Angle	0.052	0.0091	
	Exposure	-0.18	0.0704	
	Exposure.summer	0.15	0.075	
Rock cook	Intercept	-4.23	0.66	0.49
	Season	4.77	0.73	
	Angle	0.16	0.023	
	Angle.summer	-0.1	0.026	
	Smooth rock	-3.32	0.73	
	Smooth rock.summer	4.05	0.87	
	Exposure	-0.29	0.13	
	Exposure.summer	0.31	0.14	
Corkwing	Intercept	-1.028	0.25	0.27
	Season	2.049	0.28	
	Rubble	1.14	0.44	
	Broken rock	-6.876	2.072	
	Broken rock.summer	7.58	2.32	

3.4.2 Effect of temperature and salinity

Figure 17 shows the mean monthly water temperature and salinity in each subarea throughout the study period. Temperatures were lowest in February (0.2-7°C, mean 4.9°C) and highest in August (13-18°C, mean 15.7°C). The temperature range was greatest near the surface, varying from slightly above the freezing point to about 18°C; at 5 m temperatures ranged from about 4 to 18°C. Salinity ranged from 0.4 to 33 near the surface, increasing to 23-35 at 5 m depth. Amplitude in salinity was greatest towards the head of the fjord (Figure 17), due to increasing freshwater influence. Salinity in the innermost parts of the fjord was lowest in the summer when runoff from the power plant was at its highest. The mean temperature in both seasons increased several degrees (winter: 7.5→9.6°C; summer: 10.4→12.9°C) and the mean salinity decreased slightly (winter: 27.8→24.7; summer: 25.3→21.9) from 1987 until 1989 (Figure 18).

The relationship between temperature/salinity and wrasse abundance is shown in Figure 19. The variables were only measured on 174 out of 299 beach seine stations (Appendix 2), and their effect on abundance is therefore analysed separately, using only seine catch data. Catch rates increased significantly with increasing temperature for both size groups of all three species. Salinity generally did not appear to have an effect on catch rates. The effect of temperature was overall strong, with up to nearly half of the residual variation in the catch data explained by this factor (Table 11). For 0 group corkwing the temperature effect was relatively small ($r^2 = 0.06$), but for these individuals a slight but significant positive association with salinity ($r^2 = 0.07$) was also found. A model combining the effects of temperature and salinity still only explained about 18% of the variation in catch rates of 0 group corkwing (Table 11).

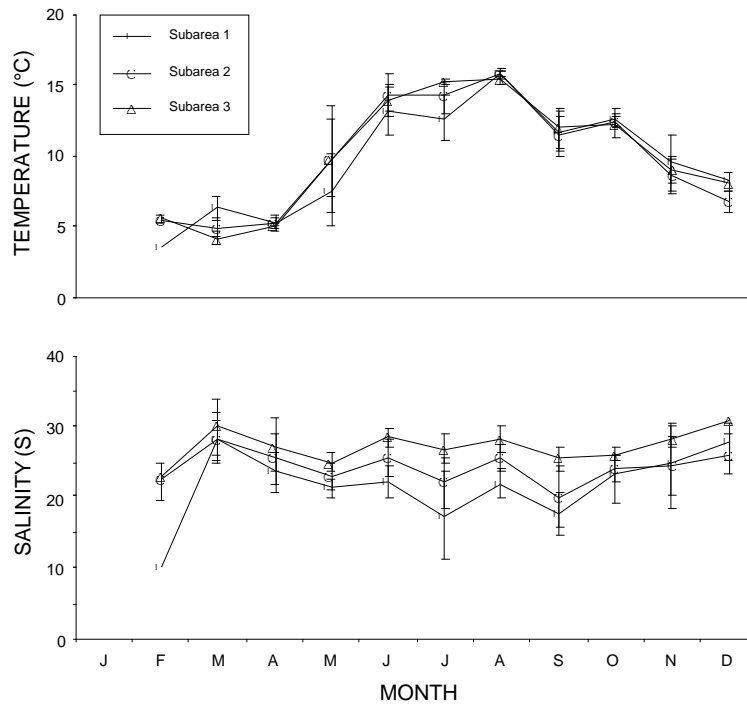


Figure 17 - Seasonal variation in temperature and salinity between 0 and 5 m depth in Masfjord. Means (\pm SD) per month in each subarea.

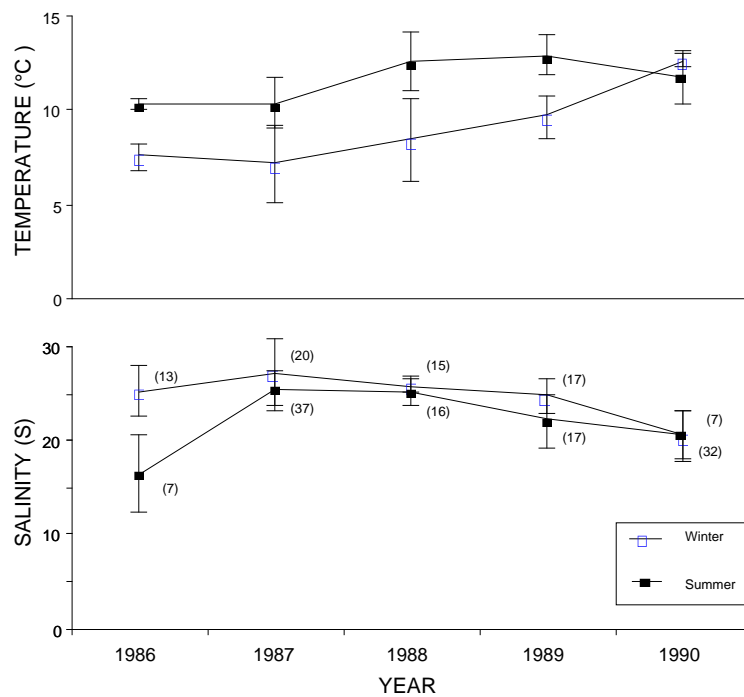


Figure 18 - Annual variation in temperature and salinity between 0 and 5 m depth in Masfjord. Means (\pm SD) per year for each season. Numbers in parentheses indicate the number of samples.

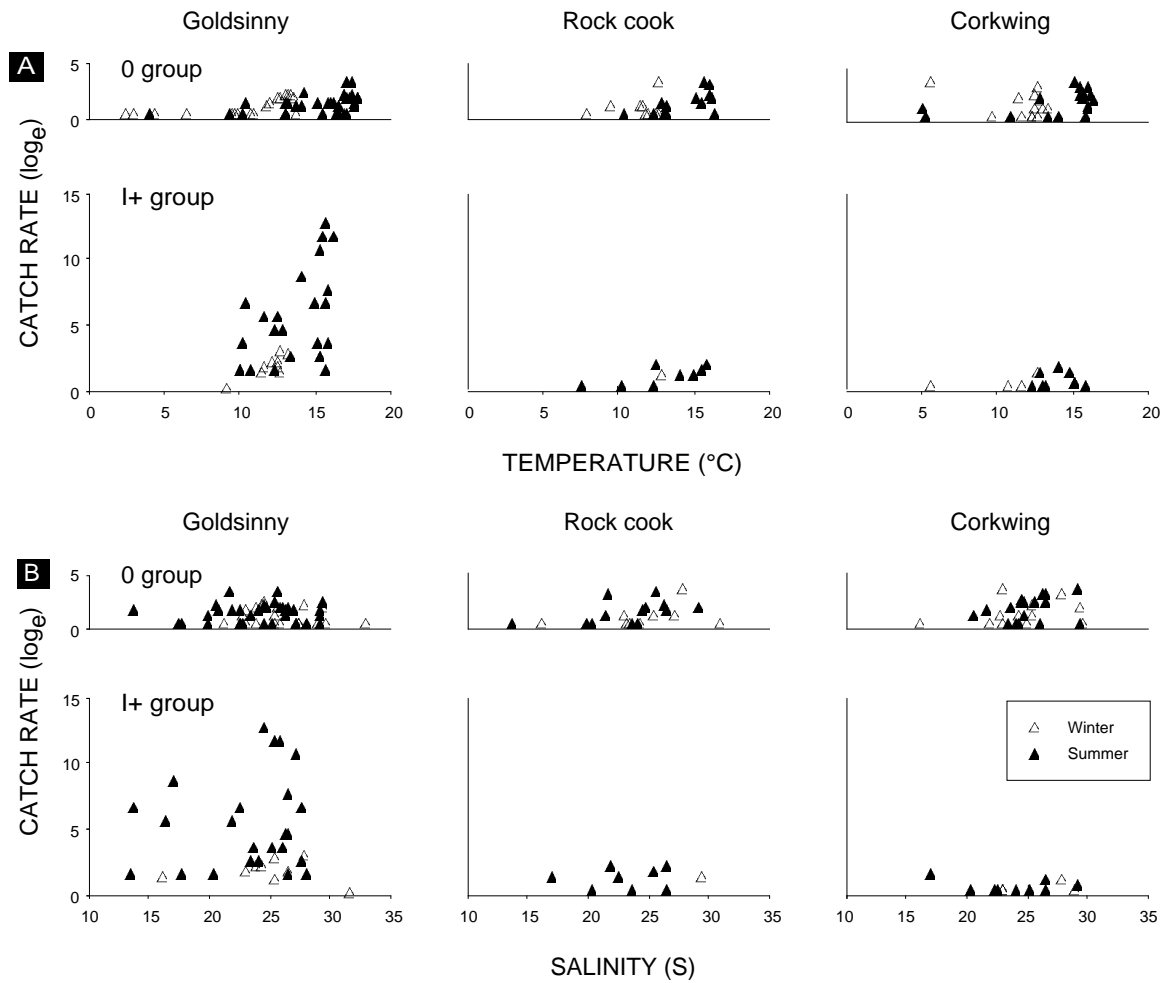


Figure 19 - Relationship between the number of wrasse in beach seine samples (log_e scale, zero catches omitted) and temperature (A) and salinity (B).

Table 11 - Effect of temperature and salinity on beach seine catch rates of 0 and I+ group wrasse. Maximum likelihood \log_e parameter estimates and standard errors of significant model terms, and percentage explained variation (r^2) from each model.

Species	Model term	Parameter estimate	Standard error	Coefficient of determination (r^2)
0 group				
Goldsinny	Intercept	-4.15	0.52	0.28
	Temperature	0.33	0.043	
Rock cook	Intercept	-6.64	0.75	0.28
	Temperature	0.47	0.059	
Corkwing	Intercept	15.12	3.30	0.18
	Temperature	-1.71	0.32	
	Salinity	-0.70	0.14	
	Temp.salin	0.076	0.013	

I+ group				
Goldsinny	Intercept	-6.68	0.67	0.41
	Temperature	0.56	0.053	
Rock cook	Intercept	-6.55	0.74	0.23
	Temperature	0.39	0.058	
Corkwing	Intercept	-5.72	0.69	0.22
	Temperature	0.33	0.053	

4 DISCUSSION

4.1 Spatial and habitat-related influences on distribution

Results from this study showed that goldsinny and particularly corkwing wrasse were distributed more towards the outer parts of the study area adjacent to Fensfjord. This is consistent with results from a faunistic survey in Hardangerfjord south of Bergen, presented in Tambs-Lyche (1987), where a reduction in numbers of labrids mainly caught by beach seine was observed from the outer to the inner fjord parts. The lack of a spatial effect in rock cook occurrence in the present study, on the other hand appears to contradict Tambs-Lyche's (1987) findings. In his study all records of this species were from the outer parts of Hardangerfjord, whereas the number of rock cook specimens collected in Masfjord seemed even slightly reduced towards the outer fjord area. The species composition and relative abundance of dominating species may, however, be drastically different even in neighbouring fjords (Brattegard 1980). Hilldén (1984) also notes that large numbers of goldsinny and corkwing may displace numbers of rock cook.

The present habitat models appear to indicate a preference in all three species for rocky and weedy biotopes over muddy or sandy biotopes with less vegetation. In a study of labrid occurrence north of Trondhjemsfjord (generally assumed the limit of wrasse distribution in Norway) Andersen *et al.* (1993) found a similar preference in goldsinny for relatively steep habitats with wrack and kelp cover. As in this study they found that catch efficiencies tended to be larger over bedrock/broken rock compared to sandy/gravelly substrata. A study on the Swedish west coast also showed that wrasse dominate the fish fauna on rocky substrata, but that they in addition are common on muddy habitats with eelgrass in outer coastal areas (Pihl *et al.* 1994). In Scottish waters the presence of goldsinny was found to be highly dependent on the proximity or availability of refuges, mainly rocks and boulders with multiple entrances (Sayer *et al.* 1993).

Aquatic macrophytes including algae and seagrass are thought to affect the distribution of many fish species, because they provide settlement habitat

and predator refuges particularly for juvenile fish (Keats *et al.* 1987, Carr 1994, Utne *et al.* 1993, Steele 1999). In wrasse, spatial variation coinciding with patterns of occurrence of macroalgae has been shown e.g. for *Tautogolabrus adspersus* (Levin 1993). In the present study only corkwing abundance was significantly affected by the presence of macrophytes, perhaps because this species uses algae as nest-building material. Abundances of the other species were more affected by bottom structure. Sayer *et al.* (1993) observed that goldsinny on the Scottish west coast appear less dependent on cover by macroalgae than on proximity of hiding places among rocks. In contrast, Hilldén (1981) showed that in an area cleared of macroalgal vegetation no goldsinny territories are established by males and foraging by females within the area is reduced. He did, however, not clearly state the nature of the substratum on the cleared area, specifically whether it provided other types of shelter.

In a field experiment with artificial seagrass units and cages in Australia, Bell *et al.* (1987) found that juveniles of the labrid fish *Achoerodus viridis* settled on artificial shelter habitat regardless of complexity, and discriminated only between shelter and bare sand with no shelter. They argue that juveniles and larvae of this species settle on the first seagrass patch they encounter, and then choose a microhabitat within that patch. In their model predation is an ultimate cause of fish abundance and distribution. Wrasse constitute one of the most preferential prey types for the larger, predatory gadid fishes in Masfjord (Nordeide & Salvanes 1991, Salvanes & Nordeide 1993). Up to 60% of the stomach contents of adult cod (*Gadus morhua* L.) and pollack (*Pollachius virens* L.) were for example found to consist of wrasse. It remains, however, to be tested whether predation on wrasse proximately or ultimately affects their distribution in Masfjord.

Results in this study showed that both yearling and older goldsinny were significantly more abundant on exposed sites, but that the degree of exposure is not a major limiting factor in explaining goldsinny distribution in Masfjord. Survey results from Øygard - a group of narrow islands south-west of Masfjord on the open coast - indicate that goldsinny occur on more exposed localities compared to the other study species (Høisæther *et al.* 1992, Høisæther & Fosså 1993). Hilldén (1984), on the other hand, found

higher goldsinny densities on sheltered compared to exposed habitats on the Swedish west coast. Nordeide *et al.* (1993) compared compositions of gill- and trammel-net catches from Masfjord and from Øygaard. There was a lower percentage especially of rock cook in the catches from Øygaard, whereas the goldsinny percentage was higher. They also found that fewer labrid but more gadoid fishes were caught in Øygaard compared to Masfjord. West-facing locations in particular in Øygaard are highly exposed to wind and waves, possibly explaining why goldsinnies are found in larger numbers here compared to Masfjord.

Juvenile goldsinnies were generally found in significantly higher abundance in the outer fjord area, whereas older individuals were mostly found within Masfjord proper, suggesting a possible ontogenetic shift in spatial association between recruits and adults. The observed pattern shift is probably not a result of adult migration across the fjord sill, since wrasse are very stationary and only move over distances of some hundred meters (Hilldén 1984). Differences in habitat utilisation were not found, indicating that such a change in association more likely is a reflection of differential survival (Green 1996)³, caused by variations in food availability or predation pressure. As for example the number of algal species increases towards the outer fjord area (Fjeldstad 1991), predator shelter availability for wrasse recruits probably also increases. Although most goldsinny eggs descend to the bottom quickly after spawning, some 10% float to the surface (Hilldén 1984) and may be carried by the surface current across the sill, aggregating in the outer archipelago. Lastly, the observed differences may also be an effect of sampling bias by the seine (see sections 4.3 and 4.5): within the fjord proper sites are generally steeper and more difficult to sample. Hence, further work needs to be done to test whether wrasse show any ontogenetic patterns in spatial association.

An indication of an ontogenetic habitat shift was observed in rock cook, where juveniles tended to have a higher degree of association with mudflats, whereas older fish seemed more associated with rocky shores. Rock cook are sometimes associated with *Zostera* beds (Wheeler 1969) mostly found

³ Green (1996) also points out that *similar* association levels may be the result of differences in survival rates.

on muddy substrata. Juvenile rock cook may rely on eelgrass for predator shelter.

4.2 Temperature and salinity as abundance limiting factors

The occurrence and abundance of all three species was markedly higher in the summer season when water temperatures were much higher compared to winter. Correlation with temperature (Figure 17a) was positive, with the effect of this factor linear and explaining much of the variation in the catches (Table 11). Water temperature greatly controls the rate of metabolic processes in fishes, and hence determines the level of activity (Pitcher & Hart 1982). The activity of wrasse in the cold season should thus be expected to be much lower than in the summer, as evidenced by the low occurrence of wrasse in the winter catches, particularly for the passive net sampling gears which rely on foraging activity.

Sayer & Davenport (1996) report that, when subjected to a rapid temperature reduction from 10 to 4°C, goldsinny wrasse entered a hypometabolic, non-reactive state of torpor. Torpor in goldsinny has also been observed during the winter in Irish waters (Sayer *et al.* 1994), where individuals were found wedged into shallow rock crevices. Winter temperature reductions in Norwegian waters are of a similar or greater magnitude, so fish remaining in shallow water should equally be adapted to quick changes in temperature. Sayer & Reader (1996) report high survival of summer-caught goldsinny subjected to wintery temperature conditions, whereas rock cook and corkwing survival was low.

The minimum temperature at which most of the wrasses in this study were caught was about 8°C. This would agree with field observations from Ireland (Darwall *et al.* 1992), Scotland (Sayer *et al.* 1993) and Norway (Skog *et al.* 1993), which indicate that wrasse activity is restricted to temperatures above 7-9°C. Few wrasse are found actively foraging below 10°C in natural environments (Costello *et al.* 1995), but Hilldén (1984) observed goldsinny feeding at temperatures down to 5°C in aquaria, only below which they assumed a torpid state. On the other hand, Jørstad *et al.* 1993 found seemingly active and foraging goldsinny in winter near rocky shelter in Fanafjord, western Norway. Their stomachs contained some bivalves and crus-

taceans, but the individuals showed no interest toward baited pots. In this study some goldsinny were caught by beach seine at temperatures as low as 3.9-5°C, but although they were likely torpid, the present data do not permit conclusions about their activity level.

Although no supportive data are available, the lengthening photoperiod in the spring, coinciding with an increase in temperature, may be co-responsible for the spring/summer increase in wrasse activity (Sayer *et al.* 1993). As wrasses normally forage by day and rest at night (see section 4.4), it is probable that the pattern of high/low activity mirrors the daylight duration, which midwinter in Norway is short or absent, as well as the temperature regime. The most noticeable increase in wrasse abundance in the samples occurred, however, from May on, when the photoperiod in western Norway is already well on its way to its maximum length. This suggests that temperature is a more important factor influencing wrasse abundance levels.

In this study only catches of 0 group corkwing appeared to be negatively influenced by low salinity levels, but this effect was relatively small. Quignard (1966) found that corkwing and goldsinny fed at salinities as low as 12 at temperatures of 18-20°C. However, as Sayer *et al.* (1996) point out, their salinity tolerance is probably less in colder Nordic waters. Riverine input in Masfjord may be high especially in winter, but freshwater influence is minimal below 5 m. Wrasse including rock cook may thus avoid unfavourable salinity levels by withdrawing to deeper water. Sayer *et al.* (1996), however, reported regular winter catches of corkwing in freshwater-influenced shallow bays. Juvenile corkwing were in this study also captured by beach seine during winter in some sheltered bays, but these are from the outer subarea where the freshwater influence is small. Adult corkwing appear to remain active and feeding during the winter (Sayer *et al.* 1996), and show indications of seasonal adaptation to low water temperature and salinity (Sayer & Reader 1996).

4.3 Study limitations and bias

The main objective of this study was to describe patterns in the distribution of goldsinny, rock cook and corkwing wrasse in relation to a range of typical habitat features for a small fjord region. Since the range of eco-

logical tolerance of a species is often greater than can be measured in a localised, and often short-term, isolated habitat-association study (Wolff 1995), results from the present study are probably only relevant on a sub-population level. Samples from exposed environments like kelp forests, which have been shown to be an important habitat for wrasse and other fish on the west coast of Norway (Høisæther *et al.* 1992, Høisæther & Fosså 1993), were for instance under-represented in the material. Results from the present study may therefore have only little predictive power for wrasse populations in western Norway. On the other hand, the multi-annual approach to the habitat models in this study could make application of the results appropriate on a general basis, at least for similar fjords in the region (e.g. Hardangerfjord).

Sampling in this study was not designed for the purposes of habitat-association analysis, but was primarily used as a tool for quantitative population analysis of gadoid fish and their prey. The net fishery during the Masfjord Project was thus based on a random sampling strategy in order to obtain population estimates for the whole fjord (Salvanes 1991, Salvanes & Ulltang 1992). However, since many locations were sampled repeatedly by nets during the study period, and many of these locations also were sampled by beach seine, a manageable number of study sites could be isolated from the material and surveyed by scuba. Although the position of each net sampling station was marked on charts, the map scale made it difficult to pinpoint the exact location where the nets were set. The area over which the beach seine was hauled may have varied somewhat over time, but efforts were made to sample the same shore distance (Fosså 1991). Total sampling area should thus be more sharply defined for the beach seine than for the nets. Replicability testing for the beach seine also yielded similar numbers of gobies from sets of two close hauls (Fosså 1991).

To compensate for the uncertainty in determination of total sampling area, survey results were averaged over a relatively wide area of up to 60 by 20 m. The scale on which the habitat attributes were quantified was similarly wide, using only a small number of variable levels. The number of net samples from each site varied to some extent due to the randomness of the initial sampling design, and the small number of samples on some sites may have influenced the results from the modelling. However, samples from two

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or more sites were usually pooled by a classifying variable in the models, providing sufficient degrees of freedom for statistical analysis.

University diving regulations and scuba safety limits made it advisable to switch divers between survey sites and/or transects. Each of the two experienced co-divers was instructed on algal species identification and variable assessment and scale, but no between-diver calibration was performed due to time limitations. However, diver-to-surface communication was used on each separate dive in an effort to control errors and bias in the habitat assessment. Remaining between-diver bias was probably limited because of the broad variable measurement scale.

Most researchers studying the habitat utilisation of animals use a subjective evaluation of some relatively distinct environmental qualities of an area to describe the different habitat types. Since a number of classifying variables were quantified at each site during the study site survey, an attempt was made to identify habitat types from analysis of a site-similarity matrix computed from the variable estimates. Although the index of similarity and the clustering algorithm used on the resulting matrix were numerically computed, and are both often applied in ecological studies, the choice of methods greatly affects the outcome, e.g. in the shape and interpretation of the cluster diagram.

The habitats that were identified on the study sites showed a great deal of similarity on the scale of the classification variables, at least for the fjord proper (subareas 1 and 2). Only two distinct groups of habitat could basically be distinguished in this area: i) low to moderately exposed, steeply inclined locations with rocky and weedy bottoms and ii) sheltered, shallow locations with muddy and sandy bottoms and a patchy vegetation. The small number of discrete habitat types within the fjord proper seems to be in accordance with Brattegard (1980), where fjords are characterised as almost closed ecosystems showing less variability than the open coast or ocean, although they are also recognised as having a diverse flora and fauna within the various habitats. Outside the fjord sill (subarea 3) conditions were generally more like the open coast, especially on the two outermost sampling sites (sites 19 and 20), where high exposure to wind and waves provides a good environment for kelp forest vegetation.

Hauling of the beach seine required locations which are not too steep or slippery (Fosså 1989), thus excluding a high percentage of the Masfjord shoreline. In addition the bottom had to be relatively smooth so that the seine netting did not get snagged by macroalgae or cut by rocks. Setting of the nets also precluded sampling in some of the steeper sections of the fjord (Salvanes *et al.* 1991). This may have limited the range of the habitat-related variables, and consequently the number and types of habitat that could be identified.

Species identification in the studied wrasse was relatively straightforward because of distinct differences in morphology, colouring and markings (e.g. the 'eyespot' of the goldsinny and the corkwing, see Figure 1). However, in the smallest specimens differences were not so clear, and errors in distinguishing between for example juvenile corkwing and juvenile Ballan wrasse may have occurred. If specimens are fixed in formaldehyde, as the beach seine samples were, it is vital that species identification takes place before fixation and storage, because colour and even 'eyespot' disappear with time.

4.4 Temporal variation in availability

The availability of fish to capture depends for both active (e.g. seines) and passive fishing gears (e.g. bottom nets) on the swimming activity of the fish. Swimming activity in wrasse depends on territorial or egg-guarding behaviour, on foraging behaviour, and on water temperature (Alvsvåg 1993).

The gillnet catches in this study were to a great extent dominated by rock cook, probably because this species tends to actively aggregate and forage in shoals. This shoaling behaviour appears to be confirmed by its catch distributions, which were all highly 'contagious' (high variance-to-mean ratio, low k), thus likely indicating a high degree of aggregation. Aggregation in this species was also observed by Costello *et al.* (1995) from scuba census of wrasse activity in Ireland. They found that rock cook were more often contagiously distributed than the other North European species.

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Goldsinnies are permanently territorial (Hilldén 1984), with dominant males investing considerable effort in patrolling and defending relatively small territories (0.5-2.0 m², Hilldén 1981), especially during the reproductive season. Foraging by these large males is basically confined to the territory (Hilldén 1981) or within a 5 m limit (Collins 1996), possibly explaining the relatively low number of goldsinny individuals caught by the trammel-net (n = 60, Table 5). The smaller male and female goldsinnies are home-ranging and often forage in shoals over a wider area, and so should normally be more available to capture by smaller-meshed nets like the gill-net.

Alvsvåg (1993) compared sex-ratios of rock cook and corkwing caught by gillnet and trammel-net in Masfjord, and found that the male-to-female ratio in catches during the spawning season was higher for rock cook. Male corkwing guard their nesting sites, and should like goldsinny be less available to capture during this time. The probability of capture is, however, likely higher for corkwing than for goldsinny, because corkwing males have larger territories (> 15 m², Costello *et al.* 1995). Territorial and nesting behaviour is thought to occur in rock cook as well, but this is probably not as marked as for corkwing.

Wrasse typically show a strong diurnal activity pattern, with high activity during the day and retreatment into a largely inactive state within refuges during the night (Olla *et al.* 1974, Nickell & Sayer 1998). Observations on sublittoral reefs in Ireland and Scotland have shown the activity of goldsinny to peak between dawn and midday, afterwards declining towards dusk (Costello *et al.* 1995, Nickell & Sayer 1998). Foraging activity is controlled by the systemic need of the fish, and consequently its level of hunger (Hart 1986). Wrasse are probably feeding-motivated after a night spent resting, and have decreased activity during the day when the food is digested, with an increase in appetite at the end of the day.

Rock cook and corkwing most likely have a diel activity pattern similar to goldsinny. There is no information available on activity patterns from the present material, but beach seine samples were taken at varying times during daylight hours when the wrasse are known to be active. The hour at which the nets were set varied, from early morning until late evening, but

they were always retrieved between dawn and midday the following day. The soak-time interval should thus have covered at least one period of higher or peaking foraging activity in the wrasse.

Only few wrasses were caught in the winter, the majority of which were juveniles. Hilldén (1984) assumed that older wrasse migrate to deeper water, whereas juveniles remain behind in shallow water, but are inactive or in a state of torpor. Migratory behaviour has been shown conclusively in adult individuals of the North American temperate-water labrid, *Tautoga onitis* (Olla *et al.* 1980). However, scuba observations (Sayer *et al.* 1993, Skog *et al.* 1994, Costello *et al.* 1995, pers. obs.) in Scotland, Norway and Ireland indicate that both juveniles and adults of all three study species are present in shallow water throughout the cold season, but that they are in hiding and inactive at temperatures below 5°C (see section 4.2). Application of the anaesthetic quinaldine in the Scottish sublittoral revealed winter densities similar to summer densities of wrasse and other species not normally observed during winter (Sayer *et al.* 1993), thus opposing the earlier Hilldén (1984) hypothesis of wrasse migrations in Nordic waters.

An abundance peak in beach seine catches from 1988 was observed for all three species. This top was especially pronounced for 0 group recruits, and was also observed for the two-spot goby *Gobiusculus flavescens* (Fabricius) (Fosså *et al.* 1994). Both the mean overall summer and winter temperature in the area increased at least two degrees during the whole period (Figure 16), and may have had a positive effect on 0 group recruitment and activity levels. The temperature rise may also have had a positive macrophyte growth effect, thereby increasing the shelter availability for the new-settled recruits. Coastal upwelling causing an advective current in the upper fjord water layers (Aksnes *et al.* 1989) may have resulted in increased amounts of zooplankton available as food items to fish larvae, juveniles and small fish, and hence a higher survival rate for wrasse recruits and gobiids. The lower level of recruitment over the next years (1989-90), despite even higher water temperature, may be due to factors like density-dependent mortality, adult competition or increased predation pressure. Mass releases of juvenile cod in 1988 and 1989 as part of the cod enhancement project in Masfjord (Fosså *et al.* 1994) may also have resulted in lower wrasse recruitment due to increased inter-specific competition.

4.5 Vulnerability to sampling and gear selectivity

Vulnerability to capture can be defined as the probability of a fish entering or coming in contact with a fishing gear given that it is in the path of that gear (Gunderson 1993). Selectivity can then be defined (Regier & Robson 1966, Gunderson 1993) as the probability of a fish of a given species and size being retained by the gear, given that it is vulnerable. Pope *et al.* (1975) define selectivity as any factor that causes the size composition of the catch to be different from that of the population. This was clearly seen in the narrow size range of the gillnet and trammel-net, which are more size-selective than the small-meshed beach seine. The size range of wrasses in the seine samples was thus broader, including many young-of-the-year and juveniles, and is probably closer to that of the actual wrasse populations.

Selectivity in beach seine sampling is mainly caused by gear avoidance, which in turn depends on the shape (girth, streamlining) and behaviour of the fish (fright response, distribution in the water column), on the dimensions and properties of the net, and on the nature of the substratum over which the net is hauled (Hamley 1975, Parsley *et al.* 1989). Many reef fish like wrasse adapted to foraging in rocky biotopes are highly manoeuvrable, but relatively weak swimmers (Hilldén 1984), typically using only their median and paired fins for propulsion (Wootton 1990). Especially young-of-the-year may thus not be fast or mobile enough to avoid the seine, which would account for the large proportion of these individuals in the seine samples. Because swimming capability is also related to fish length (Regier and Robson 1966), larger-sized wrasses may be able to escape by swimming e.g. around the seine net ends (Parsley *et al.* 1989). Fosså (1989) compared beach seine and drop-net catches in Masfjord, and found that the seine underestimated abundances of benthic fish like wrasse, because it was not able to penetrate the algal cover, but slides over it. Similarly, Lyons (1986) observed lower seine catch efficiencies for benthic fishes than for midwater species.

For nets the most important factors causing selection are the mesh size, the behaviour of the fish, its morphology, and how it is caught by the gear (Hamley 1975). Gillnets catch fish mainly by wedging (mesh stuck tightly

around the fish body) or gilling (mesh caught behind the operculum). Bjordal *et al.* (1993) found in comparing different net mesh sizes on wrasse that the mesh twine will normally first get caught behind the preoperculum for a particular minimum fish size. Trammel-nets, which are equipped with an outer and an inner panel of meshes, catch fish by entangling in addition to wedging and gilling. Because large fish have a greater probability of being entangled than small fish, trammel-nets are regarded as less size-selective than gillnets. The smaller-meshed gillnet was generally more efficient than the trammel-net in catching the relatively small study species. For the corkwing there was no difference in efficiency between the nets, which is presumably a reflection of its comparably deeper body form (Figure 1), making it more effectively held by both mesh sizes.

4.6 Statistical methodology and related parameters

Analysis of the catch data was done by means of generalised linear modelling (GLM). GLM is a relatively recent development in statistical analysis, and constitutes a modern and powerful, unified approach to statistical techniques (Nicholls 1989, Crawley 1993, Horbowy 1994). Many of the assumptions of classical ANOVA and linear regression may be relaxed in GLM, making GLM appropriate for many types of biological data, including data from ecological surveys (e.g. Nicholls 1989, Crawley 1993) and fisheries research (e.g. Sparholt 1990, Munch-Petersen & Bay 1991, Stéfansson 1996, O'Brien & Kell 1997).

The basic assumptions of parametric procedures based on the normal distribution are: i) approximately normal errors in the data, ii) constant error variance (= homoscedasticity) and iii) a linear relationship between the response variables and the explanatory variables (= additivity in effects) (Crawley 1993, Zar 1996). In analyses of fishery data, assumptions (i) and (ii) do normally not hold true, as catch distributions are frequently highly aggregated and the standard deviation often is proportional to the mean. Furthermore, the normal probability distribution is associated with continuous variates that can take on any possible value within a plausible range, whereas catch data are most often discrete (and non-negative) counts. Transformation of the response variable - a logarithmic transformation is commonly used with net catch data (Power & Moser 1999) - may often

correct for non-normality and heteroscedasticity, but because of a high frequency of zeros in the present catch data, the asymmetry in the catch distributions would not be sufficiently corrected for. Although for example analysis-of-variance has been shown to be robust enough to tolerate a certain deviation from the requirements of normality and homoscedasticity, analyses of catch data can be handled more elegantly in GLM by specifying an error distribution and link function that fit the data and models more closely. Thus a Poisson error structure and log link is generally assumed appropriate for count data, and a negative binomial (NB) error is considered appropriate when there is overdispersion in the variance from the counts. Pennington (1996) also proposes the Δ -lognormal distribution as a good approximation to skewed abundance data from marine surveys.

A Poisson error term was assumed in models of non-zero catch data, with Pearson's χ^2 overdispersion adjustment on the standard errors of the model parameters. White & Bennetts (1996) conclude that Poisson regression models perform poorly compared to NB models when overdispersion is present in the data. Even when the overdispersion was corrected for in their data, type I error rates exceeded 5%. However, it seems less desirable to assume a NB error in a model where zeros are removed from the data. Estimation and interpretation of the dispersion parameter k is also less apparent in such a truncated distribution. The NB is considered a reasonable probability distribution for the overall description of net catch data (Power & Moser 1999). Goodness-of-fit tests also showed a number of the beach seine and net catch distributions in this study to be well approximated by the NB.

Generalised linear models (GLMs) with a NB error term need to have a constant parameter k set beforehand; a fixed value of k was therefore estimated from the catch-frequency distributions of each species. A problem with this procedure is that k is better estimated as a model parameter, to allow for different fits of the covariates in the models (Power & Moser 1999). However, the models are then technically not GLMs, because the NB error distribution used in the models is no longer a member of the exponential family of distributions. The use of fixed k 's may have biased the standard errors in the models somewhat, but statistical procedures performed with these models are probably as robust as for models using transformed variates. Power & Moser (1999) compared NB linear models and t -tests

on untransformed and log-transformed simulated data, and found that the NB models appeared to perform better in discerning differences between groups than the other models. Type I error performance appeared to be acceptable for both methods, even for small samples.

The NB dispersion parameter k is often used as an ecological indicator of aggregation in a species (Southwood 1966). Estimations of k from the present catch-frequency distributions accordingly seemed to suggest that all species were highly aggregated. Some authors (e.g. Taylor *et al.* 1979) nevertheless have criticised this use of k , because of practical inconsistencies in behaviour of the parameter, regardless of the fit of the NB. As the wrasse catch-frequency distributions varied in goodness-of-fit to the NB, any ecological interpretation of k should thus be used cautiously. The use of the k -related clumping parameter λ as an ecological indicator should likewise be cautioned against. Low values of this parameter for the present data seemed to suggest that aggregations are caused by environmental factors rather than by active (e.g. social) behaviour of the species. The use of λ was first suggested in Southwood (1966) for insect populations. Social and other behavioural patterns in fish communities - e.g. territory establishment, mating rituals, spawning aggregations - are much more complex, making it highly unlikely that distributions of e.g. wrasse should be influenced by environmental factors alone. Lastly, little subsequent work seems to have been done using the λ parameter.

4.7 Summary and conclusions

The species exhibited a great deal of overlap in their distribution, both in time and space. Occurrence and abundance in the samples was highly dependent on season, all three species being most active and available to capture during the summer season, while assuming a state of inactivity at lower winter temperatures. All appeared to be more associated with the structurally more complex rocky and weedy habitats over the non-sheltered and sparsely vegetated mudflat habitats. The only indication of a differential preference was found in the stronger association of corkwing with the algal belt. Goldsinny and rock cook appeared more influenced by the degree of rockiness of the substratum.

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In the context of this study there may be several explanations for this high level of coexistence: (i) the relatively broad scale at which the variables were measured may have made detection of differential degrees of habitat association difficult. Do the species perhaps exhibit microhabitat rather than macrohabitat preferences? (ii) niche partitioning: the species share the same habitat, but may differ in their use of other resources, e.g. food.

i) Many reef fish like wrasse show distinctive patterns of habitat use at a fine spatial scale (Green 1996). Studies on microhabitat utilisation of fish are often better studied by underwater observation rather than sampling (Costello *et al.* 1995). Diver surveys using visual census (counts) along e.g. line transects within defined habitats and depth zones provide more precise abundance (density) estimates than fishing gears, as well as information about fish behaviour and species interactions. Some methodological bias exists, however; diver estimates of wrasse abundance in Ireland were for example limited by low densities per transect (particularly for rock cook and corkwing) and underestimation of numbers of small (< 5 cm) individuals (Costello *et al.* 1995). A number of fish population surveys in northern Europe have used scuba (e.g. Jansson *et al.* 1985, Sayer *et al.* 1993), but fine-scale abundance patterns of e.g. wrasse appear not to have been studied specifically. Further work on (micro)habitat association of wrasse in Norwegian fjords should thus preferably be done using density data from diver counts, perhaps supplemented by tank trials to test for conclusive evidence of spatial preferences.

ii) In aquatic environments, trophic partitioning through morphological specialisation in prey capturing mechanisms is often more important than habitat partitioning (Ross 1986). A well-known example of the significance of trophic specialisation is from the East-African Rift Lakes where cichlids (Family Cichlidae) through competition and adaptive radiation have diversified into hundreds of species which are morphologically similar, but occupy different feeding niches (see e.g. Lévêque 1995). In the studied wrasses, which are likewise quite similar in size and build, some dietary specialisation with regard to differences in e.g. jaw morphology is also found. For example, the relatively small mouth of the rock cook enables it to feed on the small tube-living polychaete *Pomatoceros triqueter*. For the

most part of the year these wrasse are, however, opportunistic generalists in their food choice (Hilldén 1984), with a high feeding niche width (Alvsvåg 1993, Fjøsne & Gjøsæter 1996), only specialising if there is a shortage of preferred food items. For rock cook and corkwing in Masfjord diet overlap suggesting competition was found to be highest during the reproductive season (Alvsvåg 1993). High overlap does not, however, necessarily mean that inter-specific competition is high: overlap often increases with increasing prey abundance, because the prey is easier for more species to catch (Macpherson 1981).

The competitive exclusion principle (Hardin 1960) states that two species cannot coexist if survival for both is dependent on the same limited resource. Displacement by feeding competition on limited food resources does not appear to be a factor in Masfjord, judging from the high relative abundances of all wrasses throughout parts of the year. Hilldén (1984), however, notes that occurrence of rock cook is reduced when goldsinny and corkwing are common. Most likely rock cook may lose out in competition for space rather than food with the other, more fiercely territorial species. Territorial behaviour in rock cook is only observed during a short spawning period in May, prior to reproduction in the two other species (Hilldén 1984). Hilldén (1984) also concluded that there is spatial separation through differential depth distribution when all species are present. The sampling techniques that were used made it difficult to include depth as a factor in this study, but indications of the above are found in the algal belt association of the corkwing, as opposed to goldsinny and rock cook association with rocky outcrops and refuges which are more dominant below the densest algal growth zone.

5 ACKNOWLEDGEMENTS

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7 APPENDICES

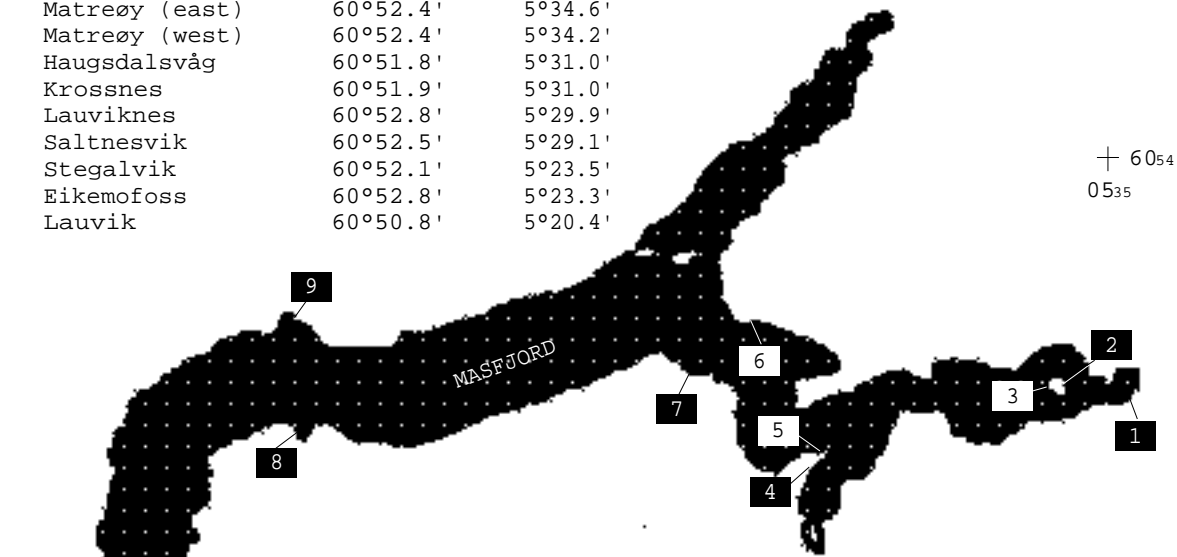
WRASSE \ˈras, -aa(ə)s, -ais\ *n* -s [Corn *wragh*, *gwragh*]: any of numerous elongate compressed but heavy-bodied usu. brilliantly colored marine fishes of the family Labridae that are related to the parrot fishes but have separate teeth in their jaws and conspicuous thick lips, that are common along rocky

Pronunciation: 'ras
Function: noun
Inflected Form(s): plural *wrasses* also *wrasse*
Etymology: Cornish *gwragh*, *wragh hag*, *wrasse*
Date: circa 1672

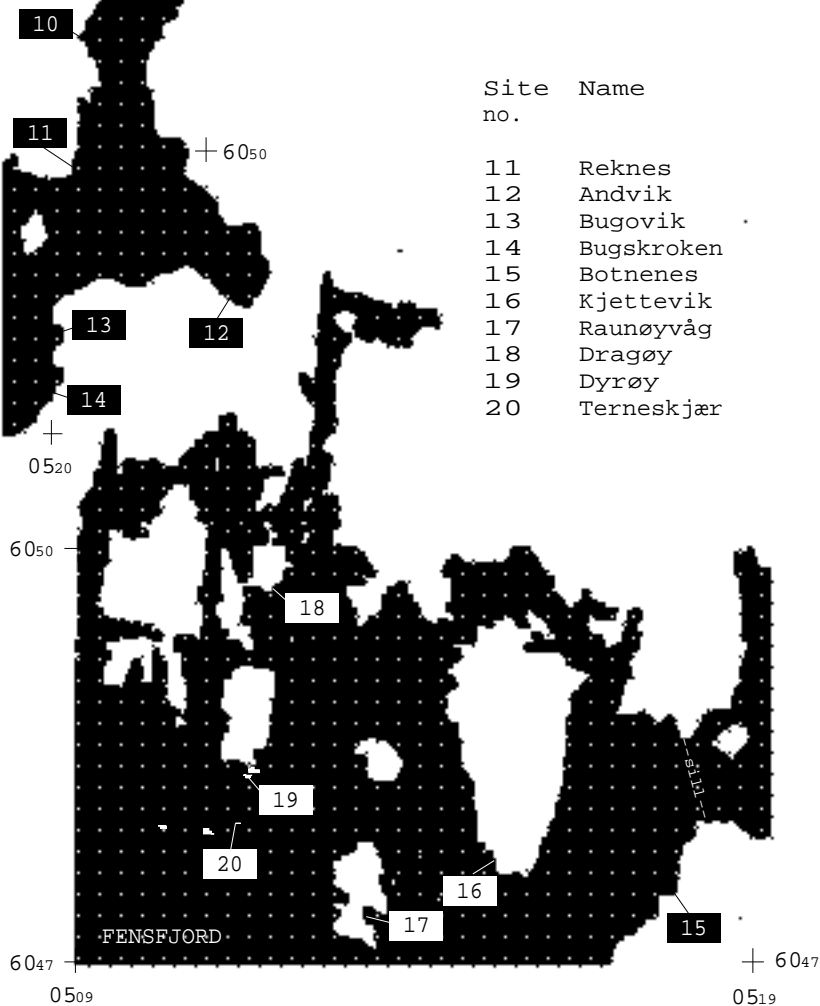
(Webster's New Dictionary of the English Language, 1971)

Appendix 1 - Study sites with chart positions.

Site no.	Name	Chart position	
1	Matre	60°52.3'N	5°35.4'E
2	Matreøy (east)	60°52.4'	5°34.6'
3	Matreøy (west)	60°52.4'	5°34.2'
4	Haugsdalsvåg	60°51.8'	5°31.0'
5	Krossnes	60°51.9'	5°31.0'
6	Lauviknes	60°52.8'	5°29.9'
7	Saltnesvik	60°52.5'	5°29.1'
8	Stegalvik	60°52.1'	5°23.5'
9	Eikemofoss	60°52.8'	5°23.3'
10	Lauvik	60°50.8'	5°20.4'



Site no.	Name	Chart position	
11	Reknes	60°49.8'N	5°20.3'E
12	Andvik	60°49.0'	5°22.6'
13	Bugovik	60°48.7'	5°20.0'
14	Bugskroken	60°48.4'	5°20.0'
15	Botnesnes	60°47.6'	5°17.6'
16	Kjettevik	60°47.7'	5°15.2'
17	Raunøyvåg	60°47.3'	5°13.4'
18	Dragøy	60°47.7'	5°11.9'
19	Dyrøy	60°48.3'	5°11.7'
20	Terneskjær	60°48.1'	5°11.4'



Appendix 2 - Beach seine sampling data. Sample label (yyymmddssnn: [yyy] year, [mm] month, [dd] day, [ss] site, [nn] subsample); time of sampling, temperature, salinity, species ([1] goldsinny, [2] rock cook, [3] corkwing), mean weight and mean length of fish in sample, catch in numbers of 0 group and I+ group wrasse. Letter indices a and b in the length-column refer to the estimation of catch per age-group for samples where length was not measured: [a] from length-weight relationship of measured samples (see section 2.5), [b] from length-frequencies of measured samples pooled for each quarter. [.] no catch.

Label	Time	Temp. (°C)	Salin. (psu)	Species	Weight (g)	Length (cm)	Catch (N)	
							0 group	I+ group
98607160701				1	11.7	b	2	4
98607160701				2		11.5	2	.
98607160702				2		b	34	7
98607161201	1700			1		3.8	2	.
98607161202				1		b	2	3
98607171701	1130						.	.
98609190701	1600	13.6	10.3	1	8.5	b	3	6
98609190701				2	1.6	a	1	.
98609191301	1100	17.6	10.1	1	8.5	5.5	1	1
98609191401	1200	17.7	10.2				.	.
98609200201	1130	15.6	10.4				.	.
98609211001	1400	13.6	10.0	1		6.0	.	1
98609211601	1145	24.3	10.9	3	0.3	a	1	.
98611170201	0830						.	.
98611170301	0900						.	.
98611170401	1100						.	.
98611170701	1230	15.7	6.6				.	.
98611171001	1530	16.7	6.7				.	.
98611171201	1330	22.0	7.6				.	.
98611181301	0900						.	.
98611181401	1000	25.6	8.2				.	.
98611181601	1115	27.4	8.3				.	.
98611181701	1200						.	.
98612151001	1430	24.1	6.2				.	.
98612151301	1230	24.6	6.3				.	.
98612151401	1130						.	.
98612160201	0930	26.1	8.0				.	.
98612160301	1010	26.0					.	.
98612160401	1100	27.6	7.8				.	.
98612160701	1155	31.5	9.1	1		10.5	.	1
98612161201	1305	29.2	7.5				.	.
98612161601	1505	31.0	7.9	2	0.1	a	1	.
98612161701	1030						.	.
98703000401							.	.
98703001201							.	.
98703110201	1045	29.5	6.7				.	.
98703110301	1135						.	.
98703110701	1415	32.8	7.2	1	0.2	a	1	.
98703111001	1545	30.8	5.6				.	.
98703121301	1530						.	.
98703121401	1430	31.5	5.7				.	.
98703121601	1100	32.8	4.8				.	.
98703121701	1145	31.5	4.0				.	.
98704070201	1045	24.9	4.9				.	.
98704070301	1200	24.4	5.0				.	.
98704070401	1315	25.5	5.3				.	.
98704070701	1430	26.9	5.5				.	.
98704071001	1630	28.6	5.9				.	.
98704071201	1745	28.3	5.6				.	.

Appendix 2

Label	Time	Temp. (°C)	Salin. (psu)	Species	Weight (g)	Length (cm)	Catch (N)	
							0 group	I+ group
98704081301	1645	30.9	4.8				.	.
98704081401	1600						.	.
98704081601	1115	30.7	4.4				.	.
98704081701	1230	30.4	5.5				.	.
98705050201	1030	21.2	4.2				.	.
98705050301	1120						.	.
98705050401	1215	21.6	5.3				.	.
98705050701	1335	23.1	5.7				.	.
98705051001	1545	23.4	6.3				.	.
98705051201	1655	21.3	6.6				.	.
98705061301	1805	21.9	7.4				.	.
98705061401	1720						.	.
98705061601	1045	24.6	7.7				.	.
98705061701	1300	26.5	7.5	2		13.5	.	1
98706090201	1300	22.2	10.5				.	.
98706090301	1430			1	10.6	10.5	.	1
98706090401	1530	20.4	12.0				.	.
98706090701	1720	21.8	12.5	1	10.6	b	3	5
98706090701				2		12.8	.	3
98706090702				2		11.0	.	2
98706091001	1945	26.2	12.3	1	10.6	b	3	4
98706091201	2020	21.2	13.5				.	.
98706101301	1605	25.7	12.8	1	10.6	7.5	.	1
98706101401	1515			1	10.6	b	4	6
98706101601	1345	26.9	13.6				.	.
98706101701	1145			1	10.6	a	.	2
98707130201	1315	24.9	12.5				.	.
98707130301	1430			1		10.0	.	1
98707130401	1515	24.5	14.4				.	.
98707130701	1650	24.1	14.8	1	13.2	10.2	.	8
98707130701				2		9.5	.	1
98707131001	1845	26.9	14.7	1	11.7	b	3	6
98707141201	1730	25.0	15.5	1	11.7	11.5	.	3
98707141301	1615	26.4	15.4	1	11.7	9.0	.	1
98707141301				2	5.3	a	.	1
98707141301				3		19.5	.	1
98707141401	1515			1		8.5	.	8
98707141402				1		9.5	.	22
98707141401				2	5.3	b	9	1
98707141601	1040	28.3	15.2				.	.
98707141701	1230			1		3.7	3	.
98707141701				2	5.3	6.0	.	1
98708190201	1330			1	9.5	a	.	1
98708190301	1430			1		9.5	.	2
98708190302				1		8.0	.	1
98708190401	1530	24.4	15.7	1		12.5	.	4
98708190402				1		b	4	8
98708190401				3	0.2	a	9	.
98708190701	2000	25.3	15.5	1	15.8	b	6	11
98708190701				2	29.4	a	.	3
98708201001	1015	27.2	15.2	1	14.6	9.1	1	10
98708201201	2030	27.6	15.7	1	28.2	11.7	.	6
98708201301	1845	27.7	15.2	1	6.8	a	.	2
98708201401	1730			1		5.8	2	2
98708201402				1		b	6	11
98708201401				3	53.4	a	.	1
98708201601	1500			1	9.6	7.0	1	2
98708201701	1400	29.2	15.2	1	2.0	5.0	2	.
98710011301	1800	23.8	12.1	1		6.5	1	1
98710011302				1		b	3	4

Label	Time	Temp. (°C)	Salin. (psu)	Species	Weight (g)	Length (cm)	Catch (N)	
							0 group	I+ group
98710011401	1715			1		10.2	.	9
98710011402				1		b	1	1
98710011601	1530						.	.
98710011701	1430	26.1	12.2				.	.
98710020201	1530			1	0.1	a	1	.
98710020201				3	0.9	a	1	.
98710020301	1615	23.9	13.0	1	0.3	a	1	.
98710020401	1330			3	0.4	a	1	.
98710020701	1200	25.4	13.2	1		8.5	.	1
98710020702				1		9.9	.	7
98710021001	1000	24.5	12.4	1	0.1	a	6	.
98710021001				3	0.1	a	7	.
98710021201	0830	24.2	12.5	1		3.5	1	.
98710021202				1		b	4	5
98710021201				2	1.5	3.5	1	.
98710021201				3	0.8	3.2	2	.
98803171001	1500	25.8	4.5				.	.
98803171201	1415	26.0	4.7				.	.
98803171301	1330			1	0.4	a	1	.
98803171401	1300	25.9	4.3	1	0.1	a	1	.
98803171601	1215	25.5	3.9	1	0.1	a	1	.
98803171701							.	.
98803180201	1030	25.0	6.0				.	.
98803180301	1000						.	.
98803180401							.	.
98803180701	0815	25.9	5.3				.	.
98804191001	1430	24.6	5.2	1	0.2	a	1	.
98804191201	1330	23.5	4.9				.	.
98804191301	1300	24.4	5.1				.	.
98804191401	1220						.	.
98804191601	1145	24.7	5.1	3	0.3	a	2	.
98804191701	1050						.	.
98804200201	1100	24.9	5.2				.	.
98804200301	1030						.	.
98804200401	0945	25.0	5.3				.	.
98804200701	0900						.	.
98805300201	1800			3	197.1	21.0	.	2
98805300301	1730						.	.
98805300401	1700						.	.
98805300701	1630			1	9.2	a	.	3
98805300701				2	19.1	a	.	4
98805301001	1515			1	30.1	12.0	.	1
98805301201	1445						.	.
98805301301	1415			3	3.6	5.5	.	1
98805301401	1345			1	21.4	10.5	1	29
98805301401				2		8.3	6	21
98805301402				2		11.8	.	2
98805301401				3		4.0	1	.
98805301402				3		b	2	1
98805301601	1300			1	18.6	9.8	.	3
98805301601				2	35.5	12.2	.	2
98805301601				3	1.2	4.2	2	.
98805301701	1230			1	0.5	2.9	6	.
98805301701				3	0.9	4.0	1	.
98806161001	1540	25.8	16.2	1	14.0	8.7	4	11
98806161201	1445	26.0	15.9	1	9.3	6.1	4	3
98806161201				3	1.6	4.5	1	.
98806161301	1345	28.0	15.6	1		13.5	.	1
98806161302				1		b	1	.
98806161401	1320			1	14.3	b	15	23
98806161401				2	2.9	b	4	10

Appendix 2

Label	Time	Temp.	Salin.	Species	Weight	Length	Catch (N)	
		(°C)	(psu)				0 group	I+ group
98806161401				3	1.0	a	2	.
98806161601	1220	29.2	14.8	1	0.6	3.5	3	.
98806161601				3	3.5	6.0	.	2
98806161701	1130			1	0.4	2.9	21	.
98806161701				2	0.8	3.6	5	.
98806161701				3	1.5	4.3	3	.
98806170201	1100	23.4	13.3	1		11.5	.	1
98806170202				1		b	2	1
98806170301	1015			1	0.9	4.0	2	.
98806170401	0930	23.5	15.4				.	.
98806170701	0840	26.4	15.9	1	16.8	9.0	4	7
98806170701				2	12.1	7.9	.	5
98806170701				3	5.6	7.0	.	1
98807200201	1145			1	0.6	2.7	3	.
98807200201				2	0.2	2.0	1	.
98807200202				2	0.1	1.0	1	.
98807200201				3	0.1	a	1	.
98807200301	1245			1	3.2	6.0	.	2
98807200301				2	0.2	2.0	2	.
98807200302				2		2.5	1	.
98807200303				2		b	4	.
98807200401	1400			1		2.0	3	.
98807200401				2	0.4	b	19	4
98807200401				3	1.1	2.7	26	2
98807200701	1545			1	10.1	7.3	1	4
98807200702				1	13.2	8.3	3	31
98807200701				2	33.6	12.0	.	1
98807200702				2	7.4	7.8	.	2
98807200701				3	0.4	3.0	1	.
98807200702				3	7.4	7.5	.	1
98807201001	1730			2	0.4	a	4	.
98807211001				1	9.5	7.7	2	16
98807211002				1		9.1	1	19
98807211001				3		8.0	.	2
98807211201	1515			1	1.8	b	2	4
98807211201				2		1.7	3	.
98807211202				2		b	5	1
98807211201				3	0.1	a	3	.
98807211301	1400						.	.
98807211401	1300			1	6.9	7.2	1	6
98807211402				1	16.4	10.1	.	8
98807211403				1	3.2	6.0	.	1
98807211404				1	11.3	8.1	.	6
98807211405				1		2.0	1	.
98807211401				2	4.1	6.2	1	1
98807211402				2	0.1	2.0	1	.
98807211403				2	8.0	8.0	.	2
98807211404				2	7.5	7.0	.	1
98807211601	1030						.	.
98807211701	0910			1		4.8	7	2
98807211702				1		b	2	2
98807211701				2	5.3	a	.	4
98807211701				3	7.1	b	22	3
98808290701	1830			1	4.5	4.6	16	8
98808290701				2	0.6	3.4	7	.
98808290701				3	1.1	3.9	6	.
98808291201	1615	25.6	15.7	1		8.0	.	2
98808291202				1		5.5	2	2
98808291203				1		4.0	1	3
98808291204				1	2.8	5.0	2	2
98808291205				1	17.0	9.5	.	2
98808291206				1	14.5	7.4	1	4
98808291207				1		2.5	6	.

Label	Time	Temp.	Salin.	Species	Weight	Length	Catch (N)	
		(°C)	(psu)				0 group	I+ group
98808291208				1		8.9	.	6
98808291209				1		4.3	2	1
98808291210				1		12.5	.	2
98808291211				1		1.9	4	.
98808291212				1		1.5	1	.
98808291201				2		3.5	2	.
98808291202				2	0.6	3.5	3	.
98808291203				2	0.5	3.1	5	.
98808291204				2		3.5	1	.
98808291205				2		2.5	1	.
98808291206				2		3.5	2	.
98808291207				2		3.0	3	.
98808291201				3		3.5	1	.
98808291202				3		2.5	1	.
98808291203				3		3.0	1	.
98808291204				3		2.2	2	.
98808291205				3		3.0	1	.
98808291301	1500	26.6	15.4	3		2.4	4	.
98808291302				3		2.8	2	.
98808291303				3		2.4	5	.
98808291304				3	0.4	2.8	3	.
98808291401	1400			1	11.2	8.6	.	13
98808291402				1		8.9	3	21
98808291401				2	0.4	2.9	8	.
98808291402				2		3.0	31	.
98808291401				3	0.7	3.2	4	.
98808291402				3		4.0	1	.
98808291403				3	0.6	3.0	10	.
98808291601	1330			2		3.0	1	.
98808291602				2		3.0	2	.
98808291601				3	0.6	3.1	5	.
98808291602				3		2.5	1	.
98808291603				3		3.5	2	.
98808291604				3		3.8	2	.
98808291605				3	0.4	2.7	3	.
98808291606				3		3.0	3	.
98808291607				3		2.5	2	.
98808291701	1230	29.1	15.2	1	10.3	6.5	1	2
98808291701				2		2.5	1	.
98808291702				2		b	3	.
98808291701				3	0.3	2.3	25	.
98808300201	1130	21.7	16.0	1	0.3	2.3	11	.
98808300202				1		2.8	6	1
98808300203				1		1.5	1	.
98808300204				1		1.8	2	.
98808300201				2		2.9	7	.
98808300202				2		2.6	6	.
98808300201				3		14.5	.	1
98808300202				3		2.8	3	.
98808300301	1050			1		3.8	8	4
98808300302				1		3.3	5	2
98808300301				2		3.5	4	.
98808300302				2		3.0	2	.
98808300401	1000	20.6	15.9	1	0.4	3.0	5	.
98808300401				2	5.9	7.0	.	1
98808300401				3	0.4	2.8	2	.
98808301001	0850	24.5	15.6	1	2.4	4.4	5	3
98808301001				2	0.6	3.5	3	.
98808301001				3	1.2	4.1	7	1
98810130201	0905			1	1.0	a	1	.
98810130301		24.9	12.3				.	.
98810130401	1015	25.0	12.2	3	1.3	a	1	.
98810130701	1130	29.3	12.9	1	2.2	a	2	.
98810130702				1	0.5	a	2	.

Appendix 2

Label	Time	Temp.	Salin.	Species	Weight	Length	Catch (N)	
		(°C)	(psu)				0 group	I+ group
98810130701				2	3.2	a	.	2
98810130701				3	1.6	4.5	3	.
98810130702				3	1.0	a	1	.
98810131001	1630	25.5	11.9	1	0.4	3.0	2	.
98810131002				1	0.2	2.2	2	.
98810131201		26.2	13.0				.	.
98810141301	0815			1	1.2	4.5	1	.
98810141301				3	0.4	3.0	1	.
98810141302				3	0.8	4.0	1	.
98810141303				3	0.6	3.2	2	.
98810141304				3	0.4	a	1	.
98810141401	1000	27.8	12.7	1	13.4	9.0	.	1
98810141402				1	0.1	2.0	2	.
98810141403				1	9.8	7.8	2	4
98810141404				1	23.0	10.5	.	1
98810141405				1	6.9	7.3	1	4
98810141406				1	25.9	11.5	.	1
98810141401				2	1.1	4.0	4	.
98810141402				2	1.2	4.2	4	.
98810141403				2	1.1	4.0	1	.
98810141404				2	0.4	3.0	1	.
98810141405				2	0.9	4.1	6	.
98810141406				2		4.0	4	.
98810141401				3		3.7	4	1
98810141402				3	0.5	3.0	2	.
98810141403				3	0.4	3.2	3	.
98810141404				3	1.4	4.5	1	1
98810141405				3		3.8	3	.
98810141601							.	.
98810141701							.	.
98812141001	1500						.	.
98812141201	1405						.	.
98812141301	1320			3	0.3	a	1	.
98812141401	1240			3	0.4	a	2	.
98812141601	1110			3	0.7	a	3	.
98812141701	1000			1	0.3	a	4	.
98812141701				3	4.3	a	.	4
98812150201	1150						.	.
98812150301	1110						.	.
98812150401	1030						.	.
98812150701	0945						.	.
98902090201	1600	10.4	3.7				.	.
98902090301							.	.
98902090401							.	.
98902090701							.	.
98902091001	1545	20.4	5.1				.	.
98902091201	1420	21.3	5.5				.	.
98902091301							.	.
98902091401	1250	25.4	5.6				.	.
98902091601	1120			3	1.1	b	7	.
98902091701	0930	22.9	5.6	1	0.3	a	1	.
98902091701				3	1.6	3.4	25	1
98905290201	2100						.	.
98905290301	2015						.	.
98905290401	1930						.	.
98905290701	1840	22.8	9.4	1	0.9	3.5	1	.
98905291001	1710	26.5	10.7	1	10.5	8.5	.	1
98905291201	1630			1	0.2	a	1	.
98905291301	1545			1	14.8	9.0	.	2
98905291401	1500	23.6	10.3	1	17.5	9.2	.	3
98905291401				2		13.5	.	1
98905291601	1405			1	14.5	9.5	.	3

Label	Time	Temp. (°C)	Salin. (psu)	Species	Weight (g)	Length (cm)	Catch (N)	
							0 group	I+ group
98905291601				3	0.8	4.0	1	.
98905291701	1300			1	12.4	7.6	5	8
98905291701				3	0.8	4.3	9	1
98907120201	1045	16.4	11.5	1	53.8	15.6	.	5
98907120301	1130						.	.
98907120401	1150	16.7	13.3				.	.
98907120701	1300	16.9	14.0	1	23.8	11.5	.	8
98907120701				2	7.5	7.5	.	2
98907120701				3	8.9	8.2	.	3
98907121001	1430	22.4	15.0	1	4.8	6.5	.	2
98907121002				1		b	3	4
98907121001				2	7.5	a	.	2
98907121201	1515	22.5	15.2	1	0.5	a	1	.
98907121201				3	10.9	a	.	1
98907121301	1610	24.0	15.2	1	8.4	7.3	.	2
98907131401	1215			1	6.4	6.9	5	18
98907131401				2	4.8	6.7	1	10
98907131401				3	18.9	9.5	.	2
98907131601	0945	25.2	15.1	1	4.3	6.5	1	3
98907131601				3	5.9	7.5	.	1
98907131701	1015			1	0.7	3.9	5	.
98907131701				2	8.2	a	.	1
98909050201	1200	20.3	12.2	1	32.6	11.5	.	1
98909050201				2		9.0	.	1
98909050202				2		b	1	.
98909050201				3	81.4	15.5	.	1
98909050301	1245						.	.
98909050401	1330	21.0	12.6				.	.
98909050701	1515	17.5	12.5	1	2.2	5.0	1	.
98909051001	1545	24.6	13.1				.	.
98909051201	1645	23.9	13.1	2	0.1	1.5	1	.
98909051201				3	110.7	17.0	.	1
98909051301	1130			1	5.7	a	.	1
98909061301				1	5.7	7.0	.	1
98909061401	1120	22.3	13.0	3	12.8	9.0	.	1
98909061601	0935			1	3.0	4.8	4	4
98909061601				2	0.9	4.0	3	.
98909061601				3	0.6	3.5	2	.
98909061701	1015	26.5	12.9	1	18.0	9.3	.	4
98909061701				2	0.1	2.0	3	.
98909061701				3	7.1	4.9	6	2
98910030201	1030	23.3	11.8	2	0.1	a	1	.
98910030301	1130						.	.
98910030401	1220	23.2	12.1				.	.
98910030701	1300	26.5	12.5	1	10.9	7.8	.	3
98910031001	1405	23.4	11.9	2	0.1	1.5	1	.
98910031201	1510	25.0	12.1				.	.
98910031301	1600			2	0.3	2.5	2	.
98910041401	1115	22.8	11.5	1	3.8	4.7	3	3
98910041401				2	0.2	a	2	.
98910041401				3	6.6	6.2	1	1
98910041601	0935			3	0.6	3.5	1	.
98910041701	1005	25.5	11.3	1	2.1	4.2	2	2
98910041701				2	0.4	3.0	2	.
98910041701				3	0.6	3.3	5	.
98911070201	1015	27.4	10.5	1	0.1	1.5	1	.
98911070301	1120						.	.
98911070401	1210	26.4	10.4				.	.
98911070701	1240	28.8	10.7	1	0.2	2.0	1	.
98911070701				3	37.5	12.0	.	1
98911071001	1400	27.0	9.8	1	0.1	a	1	.

Appendix 2

Label	Time	Temp.	Salin.	Species	Weight	Length	Catch (N)	
		(°C)	(psu)				0 group	I+ group
98911071201	1500	27.4	9.6	1	0.1	1.5	1	.
98911081301	1200	27.2	9.5	2	0.2	2.0	2	.
98911081401	1115			1	0.3	2.5	1	.
98911081601	0945			3	1.2	3.8	4	1
98911081701	1015	29.5	9.7	1	0.3	2.5	1	.
98911081701				3	0.5	3.0	1	.
99004030201	0910	19.1	5.1				.	.
99004030301	1000						.	.
99004030401	1030	20.0	5.1				.	.
99004030701	1155	21.0	5.3				.	.
99004031001	1300						.	.
99004031201	1400	20.5	5.7				.	.
99004041301	1215	22.8	5.8				.	.
99004041401	1140						.	.
99004041601	0945	23.4	5.3	3	1.0	4.0	1	.
99004041701	1020						.	.
99005140201	1030	20.6	8.3				.	.
99005140301	1115						.	.
99005140401	1145	21.6	9.3				.	.
99005140701	1230	18.9	10.8				.	.
99005141001	1350	23.4	11.7				.	.
99005141201	1445	21.4	12.4				.	.
99005141301	1530						.	.
99005141401	1600	21.4	13.3	1	12.7	8.9	.	13
99005141401				2	1.9	5.1	2	2
99005141601	1655			1	8.0	6.7	3	4
99005141602				1	15.9	8.5	.	3
99005141601				2	14.6	9.5	.	1
99005141602				2	16.4	9.5	.	4
99005141701	1730	24.0	14.1	1	0.5	3.2	3	.
99005141701				3	0.9	4.0	1	.
99006250201	1100	18.7	12.7	1	20.1	10.5	.	1
99006250301	1140						.	.
99006250401	1230	20.9	13.8				.	.
99006250701	1340						.	.
99006251001	1500	22.6	14.4	1	10.5	8.2	1	8
99006251001				2		9.0	.	1
99006251201	1600						.	.
99006261301	1230	29.2	13.4				.	.
99006261401	1130			1	6.0	7.1	.	4
99006261601							.	.
99006261701	1000	29.3	13.4	1	1.7	4.2	7	1
99006261701				3	18.7	9.2	1	5
99007120201	1145	9.3	10.7				.	.
99007120301	1230			1	15.6	8.8	.	2
99007120401	1340	9.1	10.6				.	.
99007120701	1450	13.7	11.8	1	21.0	11.0	.	2
99007120701				2	16.3	9.8	.	2
99007120701				3	43.3	13.2	.	3
99007121001	1645	18.1	12.6	1	16.9	9.0	.	2
99007121201	1800	16.5	12.8	1	22.5	10.5	.	2
99007131301		18.9	12.8				.	.
99007131401	1450	19.9	13.0	1	9.4	8.2	2	19
99007131401				2	0.1	a	1	.
99007131601	1515						.	.
99007131701				1	7.8	7.1	2	3
99008281001	1835	21.9	16.2				.	.
99008281201	1700	23.7	16.3	1	4.3	a	.	2
99008281201				2	0.1	a	1	.
99008281201				3	0.6	a	4	.

Label	Time	Temp.	Salin.	Species	Weight (g)	Length (cm)	Catch (N)	
		(°C)	(psu)				0 group	I+ group
99008281301	1505			1	8.0	7.8	.	5
99008281301				3	1.1	3.7	3	.
99008281401	1350	24.7	16.2	1	16.4	b	4	9
99008281401				2	0.7	a	4	.
99008281401				3	0.5	b	7	1
99008281601	1050	26.2	16.0	1	2.3	a	2	.
99008281601				2	0.5	b	5	1
99008281601				3	3.5	b	14	2
99008281701	1200			1	0.2	a	1	.
99008281701				2	0.4	a	3	.
99008281701				3	0.5	b	10	1
99008290201	1005	19.9	15.5	1	7.8	6.5	1	1
99008290301	1110			1	178.4	a	.	2
99008290401	1225	20.7	16.0				.	.
99008290701	1330	20.8	16.1	1	22.0	b	3	4
99008290701				3	61.0	a	.	2
99010160201	0920	20.9	12.7				.	.
99010160301	1030						.	.
99010160401	1130	17.5	12.3				.	.
99010160701	1225	16.0	12.7	1	15.1	a	.	2
99010160701				2	0.3	a	1	.
99010160701				3	2.2	a	1	.
99010161001	1345	21.3	12.4	1	0.1	a	1	.
99010161201	1510	21.8	12.3	3	2.1	a	1	.
99010161301							.	.
99010171401	1215	22.6	13.0	1	0.2	a	2	.
99010171401				3	1.2	a	2	.
99010171601	1000	25.4	13.3	3	2.0	a	2	.
99010171701	1050			1	0.2	a	3	.
99010171701				3	0.9	b	18	2

Appendix 3 - Net sampling data. Sample label (yyyymmddnnnn: [yyy] year, [mm] month, [dd] day, [nnnn] net station number); gear type ([92] trammel-net, [94] gillnet); time of setting/retrieval (Set/Retr); depth in m of shallow/deep net ends (Min/Max); catch in numbers (N) and mean length in cm of fish in sample (L) (index: [1] goldsinny, [2] rock cook, [3] corkwing). Station number and gear code as in Masfjord Project database. [.] no catch.

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98601220028	94	12	1400	0850	5	10
98601220029	92	12	1400	0850	6	20
98601220025	94	13	1350	0830	4	10
98601220026	92	13	1350	0830	6	12
98601230047	94	3	1150	0845	4	6
98601230048	92	3	0845	0845	6	22
98601230044	94	6	1450	0910	3	12
98601230045	92	6	1450	0720	5	29
98602170001	94	16	1405	0955	3	10
98602170002	92	16	1405	1000	3	14
98602170006	94	20	1510	1025	5	22
98602170007	92	20	1510	1025	4	21
98602180026	94	12	1600	1010	4	11
98602180027	92	12	1600	1010	5	23
98602180031	94	13	1525	0935	3	7
98602180032	92	13	1525	0930	4	34
98602200074	94	3	1405	1035	4	8
98602200075	92	3	1405	1045	5	8
98602200066	94	6	1500	0920	3	8
98602200067	92	6	1500	0915	6	16	.	.	1	15.0	.	.
98603170001	94	20	1345	1025	5	10
98603170002	92	20	1345	1020	10	25
98603180030	94	8	1730	1110	6	13	.	.	1	14.0	.	.
98603180031	92	8	1730	1100	12	20
98603190046	94	6	1445	0835	6	12	1	14.0
98603190047	92	6	1445	0840	8	14
98603200062	94	3	1330	0935	5	8
98603200063	92	3				
98603200049	94	5	1405	0910	6	9
98603200050	92	5	1405	0900	8	13
98604140001	94	15	1610	0911	4	11
98604140002	92	15	1610	0904	6	18
98604140004	94	16	1600	0845	5	11
98604140005	92	16	1600	0847	6	19
98604140010	94	20	1345	0958	8	13
98604140011	92	20	1345	1000	12	23
98604160050	94	11	1415	0905	3	8
98604160051	92	11	1445	0910	6	18
98604160047	94	14	1400	1040	3	12
98604160048	92	14	1400	1040	4	24
98604170079	94	3	1245	1017	3	6
98604170080	92	3	1245	1023	4	11
98604170073	94	6	1330	0936	6	13	1	14.0	5	13.0	.	.
98604170074	92	6	1330	0930	7	31
98605120006	94	16	1835	0840	4	13	2	13.0
98605120007	92	16	1835	0825	6	14
98605120011	94	19	1855	0940	3	9	2	13.0	1	13.0	.	.
98605120012	92	19	1855	0940	5	13
98605130044	94	10	1440	0740	6	13	6	13.7	1	13.0	.	.
98605130045	92	10	1440	0750	5	18
98605130036	94	12	1420	0830	5	18
98605130037	92	12	1420	0830	6	13
98605130031	94	13	1350	0815	4	8
98605130032	92	13	1350	0820	5	12

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98605140071	94	8	1430	0740	5	19	1	14.0
98605140072	92	8	1430	0740	4	20
98605150101	94	3	1235	0900	4	7	3	.	4	16.0	.	.
98605150102	92	3	1235	0900	4	10
98606160004	94	16	2105	2105	3	14	3	14.3	1	13.0	.	.
98606160005	92	16	2105	0820	6	16
98606160010	94	20	1950	0915	2	13	3	12.7	18	13.3	.	.
98606160011	92	20	1945	0920	4	13	.	.	1	17.0	.	.
98606170026	94	8	1455	0735	5	18	1	13.0	6	12.7	.	.
98606170027	92	8	1455	0730	5	15
98606180042	94	6	1145	0833	5	19	7	13.7	4	12.5	.	.
98606180043	92	6	1145	0840	2	12
98606190055	94	3	1105	0900	4	12	1	14.0
98606190056	92	3	1105	0900	4	11
98606190049	94	4	1145	0755	6	9	8	13.9
98606190050	92	4	1145	0800	9	15	.	.	1	15.0	.	.
98607020030	94	19	1210	0840	3	8	1	13.0	18	12.5	1	14.0
98607020031	92	19	1210	0850	3	13
98607040070	94	1	1420	0950	4	12	4	13.5	8	13.2	.	.
98607040071	92	1	1420	0955	5	12
98608040007	94	20	1915	1015	6	13	4	13.5	19	13.4	.	.
98608040008	92	20	1915	1000	4	13	.	.	1	17.0	.	.
98608050030	94	10	1455	0820	3	16	13	13.2	5	13.5	.	.
98608050031	92	10	1455	0810	6	18
98608050024	94	13	1420	0925	4	8	3	13.7	18	12.8	5	13.0
98608050025	92	13	1420	0920	6	23
98608060050	94	8	1840	1010	3	9	4	13.2	33	12.8	.	.
98608060051	92	8	1840	1015	4	14	.	.	1	15.0	1	21.0
98608060053	94	9	1755	0735	4	12	26	13.0	59	13.0	1	15.0
98608060054	92	9	1755	0750	3	14	.	.	3	14.3	4	18.2
98608070073	94	3	1350	0930	3	9	2	12.5	3	12.0	.	.
98608070074	92	3	1350	0940	4	7
98608070067	94	4	1420	0955	6	8	14	13.5	10	12.9	4	13.5
98608070068	92	4	1420	1010	2	11	.	.	2	14.5	19	16.8
98609230004	94	15	1340	0940	4	17	6	.	4	14.0	30	.
98609230005	92	15	1340	0920	5	14	13	17.5
98609230010	94	20	1410	1150	5	16	3	13.0	5	13.4	12	12.7
98609230011	92	20	1410	1030	5	12	.	.	2	16.0	.	.
98609240033	94	8	1645	1100	3	18	7	.	27	.	5	12.8
98609240034	92	8	1645	1035	4	7	.	.	3	14.7	6	17.2
98609240024	94	11	1500	0840	4	15	5	13.2	7	13.4	3	14.3
98609240025	92	11	1500	0830	6	12
98609250053	94	6	1325	0820	4	12	12	13.0	71	12.0	.	.
98609250054	92	6	1325	0800	3	12	.	.	4	16.0	4	15.8
98609260073	94	1	1450	1030	3	16	8	8.0	7	.	.	.
98609260074	92	1	1450	1015	3	11	.	.	4	15.0	.	.
98609260070	94	3	1500	0940	3	6	1	13.0
98609260071	92	3	1500	0945	3	6
98609260067	94	4	1515	0915	3	12	18	.	2	13.0	.	.
98609260068	92	4	1515	0900	2	13
98609260064	94	5	1520	0850	4	19	12	13.2	30	.	.	.
98609260065	92	5	1520	0830	4	23	.	.	3	15.0	5	17.0
98610280001	94	18	1530	1015	10	14
98610280002	92	18	1530	1000	9	12
98610300053	94	8	1555	1020	3	9	1	13.0	2	14.0	.	.
98610300054	92	8	1555	1025	3	15
98610300044	94	11	1530	0830	6	11
98610300045	92	11	1530	0830	6	12	1	13.0
98610300041	94	13	1500	0855	7	10	3	13.0
98610300042	92	13	1500	0900	6	11
98610310073	94	1	1415	1025	5	14	8	13.0	16	12.7	.	.
98610310074	92	1	1415	1010	5	13	1	12.0

Appendix 3

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98611110001	94	15	1515	0900	6	18	.		.		.	
98611110002	92	15	1515	0850	6	17	.		.		1	16.0
98611120024	94	11	1515	0820	6	12	2	14.0	.		.	
98611120025	92	11	1515	0805	4	10	.		.		.	
98611120030	94	12	1500	0920	3	11	.		.		.	
98611120031	92	12	1500	0925	3	12	.		.		.	
98611130047	94	9	1515	0755	2	28	2	13.5	1	15.0	.	
98611130048	92	9	1515	0750	2	19	.		.		.	
98611130044	94	10	1535	0830	2	10	.		.		.	
98611130045	92	10	1535	0835	2	14	.		.		.	
98611140073	94	3	1420	0940	3	7	.		.		.	
98611140074	92	3	1420	0930	6	7	.		.		.	
98612020013	94	18	1400	1040	6	8	.		.		.	
98612020014	92	18	1400	1045	6	7	.		.		1	15.0
98612020007	94	20	1345	1015	9	15	.		.		.	
98612020008	92	20	1345	1020	10	14	.		.		.	
98612030030	94	8	1640	1100	6	16	.		.		.	
98612030031	92	8	1640	1100	6	17	.		.		.	
98612030024	94	10	1620	1020	5	14	.		.		.	
98612030025	92	10	1620	1015	5	16	.		.		.	
98612050073	94	1	1445	1035	6	14	1	16.0	.		.	
98612050074	92	1	1445	1040	6	15	.		1	15.0	.	
98612050070	94	3	1555	1005	6	9	.		.		.	
98612050071	92	3	1555	1007	6	10	.		.		.	
98612050064	94	4	1510	0755	6	9	.		.		.	
98612050065	92	4	1510	0810	6	9	.		.		.	
98612050061	94	5	1515	0835	6	18	.		.		.	
98612050062	92	5	1515	0820	6	16	.		.		.	
98701200004	94	19	1430	1010	6	12	.		.		.	
98701200005	92	19	1430	1005	6	12	.		.		.	
98701200001	94	20	1435	1025	5	16	.		.		1	13.0
98701200002	92	20	1435	1020	12	16	.		.		.	
98701220050	94	8	1700	1050	6	15	.		.		.	
98701220051	92	8	1700	1045	6	15	.		.		.	
98701220053	94	9	1710	1100	6	15	.		.		.	
98701220054	92	9	1710	1102	6	19	.		.		.	
98701220044	94	11	1630	1015	6	11	.		.		.	
98701220045	92	11	1630	1010	6	12	.		.		.	
98701230073	94	1	1415	1020	6	9	.		1	14.0	.	
98701230074	92	1	1415	1015	6	12	.		.		.	
98701230070	94	3	1425	0950	6	8	.		.		.	
98701230071	92	3	1425	0951	6	8	.		.		.	
98701230067	94	5	1435	0935	6	18	.		.		.	
98701230068	92	5	1435	0925	6	17	.		.		.	
98701230064	94	6	1500	0905	6	13	.		.		.	
98701230065	92	6	1500	0906	6	15	.		.		.	
98702170013	94	15	1635	0845	6	18	.		.		.	
98702170014	92	15	1635	0850	6	8	.		.		.	
98702170010	94	16	1405	0920	6	11	.		.		.	
98702170011	92	16	1405	0925	6	14	.		.		.	
98702170001	94	18	1435	1100	5	8	.		.		.	
98702170002	92	18	1445	1105	5	8	.		.		.	
98702180026	94	11	1555	0825	6	12	.		.		.	
98702180027	92	11	1555	0830	6	12	.		.		.	
98702180035	94	12	1515	0955	6	9	.		.		.	
98702180036	92	12	1515	0945	6	15	.		.		.	
98702190057	94	8	1510	0855	6	13	.		.		.	
98702190058	92	8	1510	0850	17	28	.		.		.	
98702200079	94	3	1610	0950	5	9	.		.		.	
98702200080	92	3	1610	0955	5	9	.		.		.	
98702200076	94	4	1340	0913	4	9	.		.		.	
98702200077	92	4	1340	0917	4	9	.		.		.	
98702200070	94	6	1630	0805	6	10	.		.		.	

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98702200071	92	6	1630	0800	6	18
98702200073	94	7	1355	0845	6	13
98702200074	92	7	1355	0847	6	15
98703100013	94	18	1610	0825	6	8
98703100014	92	18	1610	0830	6	8
98703100007	94	20	1645	0935	6	9
98703100008	92	20	1645	0930	6	11
98703110035	94	8	1745	1100	6	11
98703110036	92	8	1745	1105	6	16
98703110029	94	10	1725	0830	6	14
98703110030	92	10	1725	0825	3	17
98703110026	94	12	1600	0920	3	10
98703110027	92	12	1600	0915	6	12	1	15.0
98703110023	94	13	1520	0840	6	11
98703110024	92	13	1520	0845	6	12
98703120057	94	5	1330	1115	6	12	.	.	1	12.0	.	.
98703120058	92	5	1330	1120	6	18
98703120054	94	6	1530	0740	6	10	1	17.0
98703120055	92	6	1530	0745	6	14
98703120051	94	7	1510	0805	6	10
98703120052	92	7				
98703130079	94	1	1300	0915	6	12	1	15.0
98703130080	92	1	1300	0920	6	13
98703130073	94	3	1345	0840	5	8
98703130074	92	3	1345	0845	5	9
98703130067	94	4	1430	0845	6	10
98703130068	92	4	1430	0850	6	8
98704060010	94	18	1710	1005	3	5
98704060011	92	18	1710	1010	3	5
98704060004	94	19	1655	0915	6	12
98704060005	92	19	1655	0919	6	12
98704060001	94	20	1645	0910	6	11
98704060002	92	20	1645	0900	4	14
98704070029	94	16	1345	0910	4	9
98704070030	92	16	1345	0915	4	11
98704080057	94	8	1400	1005	4	18
98704080058	92	8	1400	1010	4	20
98704080051	94	11	1335	0820	4	15	1	14.0
98704080052	92	11	1335	0825	4	14
98704080048	94	12	1310	0930	4	15
98704080049	92	12	1310	0930	4	13
98704090079	94	3	1315	0920	4	8
98704090080	92	3	1315	0920	4	7
98704090076	94	4	1325	0830	4	7
98704090077	92	4	1325	0830	4	13
98704090073	94	5	1335	0815	4	13
98704090074	92	5	1335	0815	4	14
98705050010	94	19	1545	0835	4	9	1	11.0	1	12.0	.	.
98705050011	92	19	1545	0830	3	11
98705060033	94	11	1640	0805	4	9
98705060034	92	11	1640	0810	4	9
98705060030	94	12	1620	0850	6	11
98705060031	92	12	1620	0855	6	13
98705060024	94	13	1400	0830	4	8
98705060025	92	13		0835	5	13
98705070050	94	8	1400	0910	3	9	.	.	1	13.0	.	.
98705070051	92	8	1400	0915	3	17
98705070041	94	10	1405	0835	3	17
98705070042	92	10	1405	0840	3	18
98705080073	94	1	1315	0930	4	9
98705080074	92	1	1315	0920	4	10
98706160010	94	20	1910	1030	2	13	.	.	7	14.1	3	14.3
98706160011	92	20	1910	1030	4	12	6	16.0

Appendix 3

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98706180053	94	6	1405	1000	4	8	1	13.0	7	13.6	.	
98706180054	92	6	1405	1000	4	14	.		1	15.0	2	15.5
98706180044	94	7	1345	0805	5	9	2	14.0	.		.	
98706180045	92	7	1345	0805	4	11	.		1	14.0	.	
98706190070	94	3	1230	0835	2	6	.		.		.	
98706190071	92	3	1230	0840	1	6	.		.		.	
98707010001	94	18	1915	0815	4	11	.		10	12.6	.	
98707010002	92	18	1915	0815	4	10	.		.		6	16.3
98707020030	94	19	1210	1005	4	14	4	12.8	.		.	
98707020031	92	19	1210	1010	4	7	.		.		.	
98707030053	94	9	1410	0820	4	26	2	13.5	.		.	
98707030054	92	9	1410	0905	2	19	1	10.0	3	15.3	2	14.5
98707030050	94	10	1355	0840	4	19	1	12.0	10	13.5	15	12.4
98707030051	92	10	1355	0820	2	12	19	14.1	10	14.5	1	
98707030044	94	11	1330	0805	4	7	2	15.0	24	13.2	1	12.0
98707030045	92	11	1330	0754	4	11	1	14.0	6	15.7	5	15.5
98707030041	94	12	1335	0720	4	11	11	13.0	13	12.6	.	
98707030042	92	12	1335	0730	4	11	.		2	14.0	2	13.5
98707040073	94	3	1145	0815	4	6	.		.		.	
98707040074	92	3	1145	0805	4	7	.		.		.	
98707040070	94	5	1155	0745	4	19	2	13.0	8	12.7	4	15.0
98707040071	92	5	1155	0750	4	23	1	14.0	.		3	16.7
98707040064	94	7	1210	0730	4	16	1	12.0	7	14.1	.	
98707040065	92	7	1210	0735	4	16	6	13.8	1	15.0	.	
98708250013	94	18	1530	0815	4	9	.		.		.	
98708250014	92	18	1530	0820	4	5	2	12.0	.		2	19.0
98708260033	94	11	2055	0755	4	9	3	13.3	.		.	
98708260034	92	11	2055	0800	4	9	1	14.0	2	14.0	.	
98708260027	94	12	2110	0930	4	11	9	14.1	3	13.3	6	14.2
98708260028	92	12	2110	0910	4	12	.		.		.	
98708260024	94	13	2040	0840	5	11	2	14.0	3	14.7	1	14.0
98708260025	92	13	2040	0850	5	10	.		.		2	18.5
98708260021	94	14	2015	0815	6	15	1	13.0	6	13.3	1	15.0
98708260022	92	14	2015	0823	4	7	.		1	14.0	4	15.5
98708280073	94	1	1130	0940	6	11	6	14.7	11	14.0	.	
98708280074	92	1	1130	0945	6	12	.		.		.	
98708280070	94	5	1150	0740	6	14	2	13.0	20	13.6	2	16.0
98708280071	92	5	1150	0745	6	16	.		1	15.0	5	17.2
98708280067	94	6	1210	0915	6	19	6	12.8	17	13.3	1	17.0
98708280068	92	6	1210	0905	6	10	.		8	15.1	4	16.8
98709140007	94	15	1850	0920	6	11	.		2	13.5	1	16.0
98709140008	92	15	1850	0923	6	11	.		.		6	17.3
98709150033	94	8	1440	1140	6	19	2	11.0	45	14.0	.	
98709150034	92	8	1440	1120	6	17	.		23	14.1	3	15.0
98709150024	94	11	1350	0830	6	9	8	13.6	1	13.0	.	
98709150025	92	11	1350	0840	6	13	.		.		8	15.6
98709150030	94	12	1400	0945	6	14	4	13.8	1	12.0	4	13.8
98709150031	92	12	1400	1000	6	15	.		.		2	16.0
98709160050	94	6	1630	0810	6	9	1	12.0	34	14.3	2	16.5
98709160051	92	6	1630	0800	6	10	.		.		.	
98709160047	94	7	1650	0900	6	10	27	13.6	27	13.7	.	
98709160048	92	7	1650	0900	6	13	.		4	15.5	.	
98709170073	94	1	1700	0845	6	11	2	14.0	2	13.5	.	
98709170074	92	1	1700	0835	6	13	.		1	16.0	.	
98709170070	94	3	1640	0815	6	10	.		.		.	
98709170071	92	3	1640	0810	6	10	.		.		.	
98709170067	94	4	1620	0755	6	8	2	14.5	.		.	
98709170068	92	4	1620	0745	6	9	.		.		2	16.0
98709170064	94	5	1610	0735	6	16	4	14.2	14	13.1	1	18.0
98709170065	92	5	1610	0730	6	19	.		.		.	
98710260007	94	13	1635	1120	4	7	.		.		.	
98710260008	92	13	1635	1120	4	7	.		.		.	
98710280073	94	15	1615	0850	5	11	.		.		.	

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98710280074	92	15	1615	0840	5	14	.		1	14.0	.	
98710280070	94	16	1420	0930	5	9	2	14.0	.		.	
98710280071	92	16	1420	0905	5	14	.		.		.	
98710280061	94	18	1530	1100	3	9	.		.		.	
98710280062	92	18	1530	1045	3	6	.		.		.	
98710290103	94	3	1545	0430	5	7	.		.		.	
98710290104	92	3	1545	0430	5	6	.		.		.	
98710290100	94	5	1535	0450	5	20	2	13.5	.		.	
98710290101	92	5	1535	0450	5	15	.		.		.	
98801190001	94	18	0815				.		.		.	
98801190002	92	18	0820				.		.		.	
98801190004	94	20	1500	0915	4	13	.		.		2	12.5
98801190005	92	20	1500	0900	4	8	.		.		1	17.0
98801210073	94	9	1510	1100	4	9	1	15.0	2	14.5	.	
98801210074	92	9	1510	1105	4	15	.		.		.	
98801210064	94	12	1415	1000	4	12	.		.		.	
98801210065	92	12	1415	0950	4	12	.		.		.	
98801210061	94	14	1350	0915	4	10	.		.		.	
98801210062	92	14	1350	0917	4	12	.		.		.	
98801220103	94	2	1555	0935	4	8	.		.		.	
98801220104	92	2	1555	0940	4	12	.		.		.	
98802230013	94	15	1100	0910	5	12	.		.		.	
98802230014	92	15	1100	0855	5	20	.		.		.	
98802230004	94	20	1125	1035	5	11	.		.		.	
98802230005	92	20	1125	1025	5	10	.		.		.	
98802240034	94	13	1315	0815	5	10	.		.		.	
98802240035	92	13	1315	0810	5	20	.		.		.	
98802250064	94	8	1250	0905	5	13	.		.		.	
98802250065	92	8	1250	0900	5	15	.		.		.	
98802250070	94	10	1150	0805	5	10	.		.		.	
98802250071	92	10	1150	0800	5	12	.		.		.	
98802260100	94	1	1320	0955	5	12	.		.		.	
98802260101	92	1	1320	0955	5	13	.		.		.	
98802260103	94	3	1305	0935	4	6	.		.		.	
98802260104	92	3	1305	0925	4	6	.		.		.	
98802260097	94	5	1200	0840	5	19	.		.		.	
98802260098	92	5	1200	0845	5	18	.		.		.	
98802260094	94	6	1130	0735	5	8	.		.		.	
98802260095	92	6	1130	0730	5	12	.		.		.	
98803220010	94	16	1200	0835	5	13	.		.		.	
98803220011	92	16	1200	0845	5	15	.		.		.	
98803220013	94	20	1245	0945	5	12	.		.		.	
98803220014	92	20	1245	0950	5	12	.		.		.	
98803230031	94	10	1425	0740	5	11	.		.		.	
98803230032	92	10	1425	0743	5	12	.		.		.	
98803230040	94	12	1240	0915	5	9	.		.		.	
98803230041	92	12	1240	0905	5	14	.		.		.	
98803240070	94	5	1400	0820	5	16	.		.		.	
98803240071	92	5	1400	0825	5	15	.		.		.	
98803250103	94	1	1150	0855	5	12	1		.		.	
98803250104	92	1	1150	0840	5	11	.		.		.	
98803250100	94	2	1200	0815	5	14	.		.		.	
98803250101	92	2	1200	0820	5	12	.		.		.	
98803250097	94	3	1130	0755	5	11	.		.		.	
98803250098	92	3	1130	0750	5	9	.		.		.	
98804120004	94	19	1405	0955	5	13	.		.		1	13.0
98804120005	92	19	1405	0940	5	11	.		.		.	
98804140074	94	8	1510	1010	5	16	.		.		.	
98804140075	92	8	1510	1005	5	15	.		.		.	
98804140071	94	9	1320	1025	5	11	.		.		.	
98804140072	92	9	1320	1020	5	15	.		.		.	
98804140083	94	13	1325	0825	5	8	.		.		.	
98804140084	92	13	1325	0820	5	8	.		.		.	

Appendix 3

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98804150113	94	1	1530	0920	5	19
98804150114	92	1	1530	0915	5	14
98805240010	94	15	1800	0900	5	15	1	12.0
98805240011	92	15	1800	0905	5	15	.	.	1	15.0	14	15.8
98805240013	94	20	1845	0830	5	13	5	12.4	5	13.0	.	.
98805240014	92	20	1845	0835	5	13
98805250043	94	11	1330	0808	5	9	7	12.6	7	12.1	.	.
98805250044	92	11	1330	0800	5	8
98805250031	94	14	1240	0823	5	9
98805250032	92	14	1240	0830	5	8	.	.	1	15.0	5	16.0
98805260073	94	8	1400	0935	5	20	4	12.2	.	.	4	13.5
98805260074	92	8	1400	0940	5	15
98805260061	94	9	1300	0750	5	23	16	12.8	1	12.0	.	.
98805260062	92	9	1300	0745	5	20	.	.	1	15.0	.	.
98805260067	94	10	1340	0825	5	21	3	13.3	1	12.0	.	.
98805260068	92	10	1340	0830	5	20	2	14.0
98805270103	94	2	1436	0715	5	12	1	13.0
98805270104	92	2	1436	0720	5	15
98806070004	94	16	1730	0905	5	15	8	13.1	12	13.2	.	.
98806070005	92	16	1730	0855	5	15	.	.	5	14.4	1	18.0
98806090073	94	5	1550	0830	5	39	9	13.4	11	13.2	.	.
98806090074	92	5	1550	0820	5	13
98806100091	94	1	1430	0835	5	11	13	12.9	45	13.3	.	.
98806100092	92	1	1430	0830	5	12	.	.	11	14.4	.	.
98806100100	94	2	1435	0815	5	7	2	14.0
98806100101	92	2	1435	0816	5	8	2	16.0	2	14.0	2	19.0
98807050001	94	18	1720	0815	4	6	.	.	7	12.3	7	14.1
98807050002	92	18	1720	0805	4	6	.	.	1	13.0	7	14.9
98807060031	94	15	1410	0830	5	18	1	12.0	27	13.4	.	.
98807060032	92	15	1410	0940	5	18	.	.	1	15.0	8	16.2
98807060034	94	16	1345	0905	5	15	7	12.6	15	12.6	.	.
98807060035	92	16	1345	0855	5	13	2	14.5	3	14.0	10	15.3
98807060043	94	19	1300	1010	5	15	6	13.5	6	13.0	.	.
98807060044	92	19	1300	1000	5	12	.	.	5	15.0	1	17.0
98807070061	94	9	1420	0755	5	14	21	13.0	10	13.7	18	13.1
98807070062	92	9	1420	0745	5	18	.	.	15	14.7	2	20.5
98807070064	94	10	1400	0825	5	17	17	13.4	6	13.3	.	.
98807070065	92	10	1400	0815	5	17	3	12.3	5	14.8	1	16.0
98807070067	94	11	1240	0845	5	9	6	12.6	47	12.8	2	13.5
98807070068	92	11	1240	0835	5	10	.	.	6	14.5	2	17.0
98807070070	94	12	1305	0915	5	9	10	13.3	3	12.7	.	.
98807070071	92	12	1305	0900	5	10
98807080103	94	3	1425	0915	4	9	1	13.0
98807080104	92	3	1425	0918	4	5
98807080100	94	5	1410	0900	5	31	1	12.0
98807080101	92	5	1410	0855	5	25	.	.	1	15.0	.	.
98807080094	94	7	1350	0815	5	9	8	12.8	4	13.5	.	.
98807080095	92	7	1350	0820	5	12	.	.	13	15.0	2	15.0
98808230013	94	18	1450	1045	5	9	.	.	4	13.2	3	12.7
98808230014	92	18	1450	1030	5	8	9	16.0
98808240031	94	11	1520	0830	5	6	4	13.3	8	.	2	13.5
98808240032	92	11	1520	0815	5	7
98808240037	94	13	1425	0945	5	8	4	13.0	1	12.0	4	11.8
98808240038	92	13	1425	0945	5	15	3	17.0
98808250073	94	8	1510	0855	5	13	5	12.8	30	.	12	.
98808250074	92	8	1510	0855	5	20	.	.	24	14.7	5	16.2
98808260103	94	1	1805	1040	5	17	6	13.8	29	14.7	1	.
98808260104	92	1	1805	1025	5	15	1	12.0	27	.	5	16.6
98808260100	94	5	1750	0950	5	11	17	13.5	22	13.6	1	12.0
98808260101	92	5	1750	0955	5	20
98808260097	94	6	1850	0750	8	21
98808260098	92	6	1850	0745	8	20	.	.	1	15.0	.	.

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98809270007	94	15	1640	0910	5	21	3	12.5
98809270008	92	15	1640	0930	5	11	.	.	1	15.0	3	17.7
98809280043	94	8	1335	1040	5	19	3	13.0	.	.	3	11.7
98809280044	92	8	2000	1045	5	17	.	.	1	15.0	.	.
98809290073	94	6	1400	0810	5	20	15	12.9	1	12.0	1	12.0
98809290074	92	6	1400	0800	5	20	4	14.2	1	15.0	3	13.0
98809290061	94	7	1430	0845	5	14	29	13.4	3	14.0	10	12.9
98809290062	92	7	1430	09	5	18	2	13.5
98809300103	94	1	1430	1000	5	16
98809300104	92	1	1430	0945	5	11	3	14.0	10	13.4	3	13.7
98809300100	94	3	1455	0920	5	8
98809300101	92	3	1455	0910	5	9
98809300097	94	4	1350	0830	5	14
98809300098	92	4	1350	0835	5	13	1	14.0
98810180001	94	18	1110	0810	5	9	2	14.5	.	.	5	12.2
98810180002	92	18	1110	0815	5	8	4	17
98810200064	94	11	1310	0820	5	8	1	14.0
98810200065	92	11	1310	0830	5	10
98810200067	94	13	1235	0850	5	11
98810200068	92	13	1235	0840	5	15
98810210103	94	1	1400	0930	5	12	10	13.6	1	13.0	.	.
98810210104	92	1	1400	0930	5	12	.	.	1	15.0	.	.
98810210097	94	5	1300	0845	5	27	1	14.0	1	14.0	.	.
98810210098	92	5	1300	0848	5	25	1	15.0
98811150010	94	15	1240	0850	5	21	2	12.5	.	.	4	12.8
98811150011	92	15	1240	0857	5	20	5	17.0
98811150001	94	18	1350	1011	5	7	7	13.0
98811150002	92	18	1350	1010	5	9	3	16.3
98811160031	94	11	1330	0825	5	8
98811160032	92	11	1330	0840	5	9	1	14.0
98811160040	94	12	1235	0955	5	9
98811160041	92	12	1235	1000	5	12
98811170073	94	8	1525	0745	5	12	1	13.0	.	.	1	13.0
98811170074	92	8	1525	0748	5	15
98811170061	94	9	1640	0930	5	12	12	13.6
98811170062	92	9	1640	0933	5	12
98811180103	94	3	1300	0931	5	7
98811180104	92	3	1300	0931	5	7
98812060064	94	6	1555	0810	2	13	2	13.0	2	12.0	.	.
98812060065	92	6	1600	0820	2	15
98812060067	94	7	1525	0855	3	21	1	14.0
98812060068	92	7	1530	0855	25	30
98812070043	94	8	1500	1040	1	14	1	14.0	9	13.3	8	13.2
98812070044	92	8	1455	1040	1	12	1	17.0
98812080010	94	15	1630	0940	2	7
98812080011	92	15	1635	0945	2	10
98812080001	94	18	1520	1115	2	5
98812080002	92	18	1530	1530	2	6	1	18.0
98812090103	94	1	1805	0855	1	10
98812090104	92	1	1805	0845	1	8
98812090100	94	2	1755	0835	1	7
98812090101	92	2	1800	0830	1	8
98812090097	94	3	1645	0805	1	8
98812090098	92	3	1650	0810	1	9
98812090091	94	5	1520	0732	2	15	1	14.0
98812090092	92	5	1525	0730	1	15
98901240001	94	18	1300	1035	5	7
98901240002	92	18	1300	1040	5	8
98901240004	94	20	1200	0840	5	11	1	13.0
98901240005	92	20	1200	0845	5	15
98901260061	94	9	1545	1030	5	17	1	14.0	2	13.0	.	.
98901260062	92	9	1545	1040	5	25
98901260067	94	11	1510	0915	5	10

Appendix 3

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98901260068	92	11	1510	0915	5	12
98901270103	94	1	1455	0937	5	11
98901270104	92	1	1455	0942	5	15
98901270100	94	3	1500	0922	5	9
98901270101	92	3	1500	0925	5	10
98901270097	94	5	1530	0840	5	17
98901270098	92	5	1530	0848	5	22
98901270091	94	6	1555	0750	5	15	3	13.3
98901270092	92	6	1555	0755	5	20
98902210010	92	15	1330	1030	5	15
98902210011	94	15	1330	1030	5	10
98902210001	94	18	1315	1130	4	7
98902210002	92	18	1315	1140	4	5
98902220043	94	11	1420	0805	5	8
98902220044	92	11	1420	0812	5	9
98902220037	94	12	1500	0949	5	13
98902220038	92	12	1500	0941	5	15
98902230061	94	8	1620	0920	5	15
98902230062	92	8	1620	0915	5	22
98902230073	94	9	1635	0735	5	10
98902230074	92	9	1635	0738	5	17
98902230067	94	10	1500	0830	5	11	1	14.0
98902230068	92	10	1500	0832	5	19
98902240103	94	1	1345	0930	5	10	.	.	3	14.0	.	.
98902240104	92	1	1345	0930	5	12
98902240100	94	3	1335	0923	5	8
98902240101	92	3	1335	0915	5	9
98903140013	94	18	1415	1005	5	7
98903140014	92	18	1415	1010	5	7
98903140007	94	20	1430	1005	5	16	1	17.0
98903140008	92	20	1430	1010	5	15	1	16.0
98903150043	94	8	1700	1020	5	17
98903150044	92	8	1700	1020	5	30
98903150037	94	10	1620	0815	5	14
98903150038	92	10	1620	0816	5	20
98903150034	94	12	1410	0945	5	11
98903150035	92	12	1410	1000	5	15
98903150031	94	13	1400	0915	5	11
98903150032	92	13	1400	0917	5	10
98903160070	94	6	1240	0845	5	9	1	14.0
98903160071	92	6	1240	0847	5	10
98903170103	94	1	0945	0852	5	9	2	13.5	3	16.0	.	.
98903170104	92	1	0945	0850	5	10	1	11.0
98903170100	94	2	1005	0845	5	11
98903170101	92	2	1005	0847	5	14
98903170097	94	3	1040	0835	5	8
98903170098	92	3	1040	0836	5	9
98903170091	94	4	1120	0740	5	10
98903170092	92	4	1120	0745	5	12
98905230043	94	11	1530	0820	5	11	1	14.0	2	12.5	.	.
98905230044	92	11	1530	0837	5	8	1	16.0
98905230040	94	12	1610	0935	5	12	1	14.0
98905230041	92	12	1610	0940	5	11
98905230034	94	13	1550	0912	5	16	.	.	1	14.0	.	.
98905230035	92	13	1550	0900	5	11	.	.	1	16.0	.	.
98905240007	94	19	1415	0840	5	8	2	14.0	27	12.7	14	11.9
98905240008	92	19	1415	0830	5	10	1	15.0	11	.	.	.
98905250073	94	8	1430	0925	5	15	4	13.0	22	14.0	5	12.4
98905250074	92	8	1430	0933	5	18	.	.	4	14.2	.	.
98905250061	94	9	1455	0753	5	11	29	13.8	11	15.2	4	12.8
98905250062	92	9	1455	0748	5	16	.	.	2	14.5	.	.
98905250067	94	10	1345	0825	5	17	8	13.2	11	14.2	.	.
98905250068	92	10	1345	0833	5	20	1	15.0	1	14.0	.	.
98905260103	94	4	1320	0902	5	11	4	13.8	6	13.7	.	.

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98905260104	92	4	1320	0906	5	15
98906140001	94	15	1910	0856	5	11	1	14.0	18	13.1	1	11.0
98906140002	92	15	1910	0904	5	18
98906150040	94	8	1500	0915	5	10	2	10.5	2	14.0	.	.
98906150041	92	8	1500	0920	5	18
98906150031	94	14	1350	0800	5	15	10	12.4	2	12.5	.	.
98906150032	92	14	1350	0810	5	20	1	11.0	4	14.5	.	.
98906160103	94	1	2115	1000	5	16	10	12.9	31	13.5	.	.
98906160104	92	1	2115	1010	5	12	.	.	22	14.1	.	.
98907040001	94	18	1420	1030	5	8	.	.	9	13.0	26	13.2
98907040002	92	18	1420	1015	5	8
98907050031	94	15	1430	0925	5	8	2	12.5	20	13.1	22	13.8
98907050032	92	15	1430	0920	5	15	1	10.0	.	.	13	15.7
98907050034	94	16	1440	0855	5	14	9	13.6	20	12.7	3	12.3
98907050035	92	16	1440	0840	5	10	.	.	6	14.3	12	15.0
98907050043	94	19	1340	1040	5	9	5	14.0	33	12.6	.	.
98907050044	92	19	1340	1045	5	10	.	.	4	15.2	.	.
98907060064	94	10	1450	0930	5	11	15	12.7	27	12.2	.	.
98907060065	92	10	1450	0940	5	15	1	11.0	9	13.9	2	15.0
98907060067	94	11	1445	0850	5	9	12	13.6	50	13.2	3	12.3
98907060068	92	11	1445	0855	5	10	.	.	1	15.0	11	16.2
98907060070	94	12	1415	0835	5	14	8	13.5	1	14.0	.	.
98907060071	92	12	1415	0840	5	12	.	.	3	13.3	3	15.7
98907070103	94	3	1455	1015	5	8	1	14.0	1	14.0	.	.
98907070104	92	3	1455	1010	5	10
98907070100	94	5	1510	0950	5	21	.	.	9	13.2	1	12.0
98907070101	92	5	1510	0952	5	20
98907070097	94	7	1620	0925	5	13	1	13.0	26	14.1	9	12.9
98907070098	92	7	1620	0930	5	12
98908220031	94	11	1930	0830	3	6	1	11.0
98908220032	92	11	1930	0840	3	7	.	.	1	15.0	.	.
98908220037	94	14	1950	0930	5	12	5	13.0	1	13.0	8	13.2
98908220038	92	14	1950	0915	5	7	13	15.8
98908230010	94	18	1606	1215	5	8	7	12.6
98908230011	92	18	1606	1205	5	8	10	15.2
98908240073	94	8	1455	1125	5	18	4	13.5	12	13.2	6	13.2
98908240074	92	8	1455	1105	5	20	.	.	24	14.8	14	14.8
98908250103	94	1	1555	0930	5	12	6	12.5	8	12.6	.	.
98908250104	92	1	1555	0923	5	12	.	.	1	16.0	.	.
98908250100	94	5	1535	0845	5	12	4	13.2	8	14.6	1	14.0
98908250101	92	5	1535	0845	5	20
98908250097	94	6	1525	0655	5	16	6	13.5	23	13.5	2	12.0
98908250098	92	6	1525	0700	5	20	.	.	5	15.2	.	.
98909120007	94	15	1630	0935	5	16	3	13.0	.	.	6	12.0
98909120008	92	15	1630	0915	5	20	.	.	2	15.5	15	15.7
98909130064	94	6	1655	0827	5	11	9	12.8	9	12.8	.	.
98909130065	92	6	1655	0830	5	20	.	.	18	15.1	.	.
98909130067	94	7	1625	0915	5	10	20	13.2	5	13.4	.	.
98909130068	92	7	1625	0920	5	12	.	.	7	15.1	2	18.5
98909140043	94	8	1730	1136	5	18	3	12.3	8	13.6	.	.
98909140044	92	8	1730	1140	5	15
98909150103	94	1	1845	0949	5	14	12	13.2	1	14.0	.	.
98909150104	92	1	1845	0959	5	12
98909150100	94	3	1830	0933	5	7	1	13.0
98909150101	92	3	1830	0924	5	8
98909150097	94	4	1755	0841	5	17	5	14.6
98909150098	92	4	1755	0846	5	12	1	18.0
98909150094	94	5	1750	0829	5	15	9	13.0	10	13.3	.	.
98909150095	92	5	1750	0836	5	22	.	.	3	14.3	.	.
98910100007	94	15	1445	0940	5	11	1	13.0	2	12.5	5	13.2
98910100008	92	15	1445	0950	5	12	.	.	1	15.0	.	.
98910130103	94	1	1825	1030	5	12	2	11.5	1	14.0	.	.

Appendix 3

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
98910130104	92	1	1825	1030	5	12
98912060043	94	1	1520	0843	5	13
98912060044	92	1	1520	0830	5	12
98912060040	94	3	1510	0904	5	11
98912060041	92	3	1510	0854	5	8
98912070073	94	8	1515	1025	5	9	1	13.0	1	15.0	1	13.0
98912070074	92	8	1515	1030	5	17
98912070061	94	9	1535	0820	5	16
98912070062	92	9	1535	0825	5	15
98912080103	94	11	1420	0735	5	8
98912080104	92	11	1420	0737	5	10
98912080094	94	13	1435	0810	5	16
98912080095	92	13	1435	0811	5	10
99001160013	94	3	1525	0835	5	7
99001160014	92	3	1525	0835	5	8
99001180061	94	15	1300	0930	5	20
99001180062	92	15	1305	0930	5	15
99001180064	94	16	1440	1100	5	15
99001180065	92	16	1445	1100	5	12
99001190103	94	8	1440	1030	5	19
99001190104	92	8	1440	1030	5	22
99001190091	94	13	1245	0840	5	14
99001190092	92	13	1245	0840	5	14
99002130001	94	1	1420	0830	5	9	6	13.5	1	13.0	.	.
99002130002	92	1	1420	0830	5	13	.	.	3	14.7	.	.
99002130005	92	2	1430	0850	5	9
99002130006	94	2	1430	0850	5	7
99002140037	94	13	1410	0840	5	10
99002140038	92	13	1410	0840	5	14
99002160091	94	8	1415	0900	5	11
99002160092	92	8	1415	0900	11	18
99003200001	94	1	1425	1010	5	11
99003200002	92	1	1425	1015	5	11
99003200004	94	2	1615	0950	5	9
99003200005	92	2	1615	0940	5	10
99003200007	94	3	1605	1030	5	7
99003200008	92	3	1605	1035	5	8
99003200013	94	5	1540	1120	5	11
99003200014	92	5	1540	1125	5	20	1	16.0
99003220094	94	16	1345	0916	5	17
99003220095	92	16	1345	0920	5	17
99003220100	94	20	1550	0901	5	14
99003220101	92	20	1550	0855	5	14
99003230073	94	8	1620	1025	5	11
99003230074	92	8	1620	1030	5	15
99003230061	94	13	1235	0804	5	10
99003230062	92	13	1235	0807	5	14
99005020064	94	20	1840	0829	5	14	1	15.0	5	13.6	7	13.0
99005020065	92	20	1840	0825	5	12	.	.	1	16.0	2	17.5
99005030034	94	13	1200	0830	5	12	3	13.7	2	14.0	.	.
99005030035	92	13	1200	0830	5	9	1	16.0	1	15.0	.	.
99005040010	94	8	1830	0825	2	27	.	.	3	13.7	.	.
99005040011	92	8	1830	0820	2	20	.	.	4	14.8	.	.
99006050091	94	1	1515	1025	5	10	3	13.3
99006050092	92	1	1515	1015	5	14
99006050094	94	3	1500	1040	5	10
99006050095	92	3	1500	1035	5	11	1	13.0	.	.	1	16.0
99006060004	94	16	1600	0920	5	17	3	13.0
99006060005	92	16	1600	0907	5	15
99007020001	94	18	1630	1050	5	9	1	14.0	7	.	16	.
99007020002	92	18	1630	1055	5	8	.	.	5	15.8	.	.

Label	Gear	Site	Set	Retr	Min	Max	N1	L1	N2	L2	N3	L3
99007030037	94	16	1515	0935	5	11	4	13.2	.		19	14.0
99007030038	92	16	1515	0945	5	20	.		.		.	
99007030043	94	19	1540	0811	5	12	1	14.0	23		.	
99007030044	92	19	1540	0810	5	15	.		4		.	
99007040064	94	12	1315	0950	5	18	.		.		.	
99007040065	92	12	1315	0940	5	15	.		.		.	
99007040061	94	13	1230	0855	5	9	.		17	13.4	.	
99007040062	92	13	1230	0900	5	11	.		3		11	
99007050081	94	3	1740	0710	5	14	.		.		.	
99007050082	92	3	1740	0715	5	10	.		.		.	
99007050090	94	7	1805	0755	5	26	2	13.0	41		12	14.2
99007050091	92	7	1805	0750	5	20	.		6	14.8	3	15.7
99008200103	94	3	1900	1020	5	8	.		1	12.0	.	
99008200104	92	3	1900	1020	5	7	.		.		.	
99008200097	94	4	1835	1000	5	8	1	14.0	.		1	16.0
99008200098	92	4	1835	1000	5	10	.		.		.	
99008210013	94	18	1730	0815	5	9	1	14.0	.		4	14.5
99008210014	92	18	1730	0815	5	8	.		.		8	15.4
99008220037	94	13	1410	0930	5	11	3	13.3	.		5	16.0
99008220038	92	13	1410	0930	5	15	.		.		6	18.3
99008220034	94	14	1355	0900	5	11	1	14.0	7	12.6	25	
99008220035	92	14	1355	0900	5	15	.		.		26	
99008230064	94	8	1925	0825	5	19	1	14.0	16		6	15.3
99008230065	92	8	1925	0825	5	20	.		.		5	16.2
99008230073	94	9	1930	0730	5	11	34		2	14.5	1	13.0
99008230074	92	9	1930	0730	5	20	.		.		3	18.0
99009170031	94	1	1950	1025	5	11	21		7		.	
99009170032	92	1	1950	1026	5	10	.		.		3	17.3
99009170034	94	3	1940	1041	5	8	.		.		.	
99009170035	92	3	1940	1040	5	8	.		.		.	
99009170040	94	4	2005	1005	5	14	.		.		.	
99009170041	92	4	2005	0957	5	10	.		.		1	19.0
99009190094	94	12	1300	0915	5	18	.		.		.	
99009190095	92	12	1300	0905	5	12	.		.		.	
99009190091	94	13	1200	0830	5	11	14		.		2	13.5
99009190092	92	13	1200	0820	5	14	.		.		5	17.4
99010090037	94	10	1600	0830	5	10	2	15.0	.		.	
99010090038	92	10	1600	0830	5	12	.		.		1	19.0
99010090031	94	13	1515	0935	5	14	4	12.2	5	13.6	.	
99010090032	92	13	1515	0935	5	10	.		1	14.0	3	17.3

Appendix 4 - Habitat characteristics. Substratum type and macrophyte cover availability (for the upper 5 m) recorded at regular intervals along three transects. Depth was recorded for calculation of the substratum angle (degrees). [Expo] denotes the degree of exposure at each site. [-] no assessment, [*] assessment, no depth recording; [+] presence, [.] absence. Underlined distance indicates the 5 m depth boundary. Numbers below refer to the frequency of occurrence of the substratum types, and numbers in parentheses refer to the levels of all variables.

Site no.	Distance (m)	Depth (m)			Angle (degr.)	Soft bottom	Rubble	Broken rock	Bedrock	Cover avail.	Expo					
1	0	0	0	0	30.6	+	+	+	.	.	.	1	1	1	0	
	5	2.7	4	4		+	+	+	.	.	.	3	2	2		
	<u>10</u>	4.3	4.5	4.5		.	.	+	.	.	.	2	1	2		
	15	7.5	7.5	7.5		+	+	+	.	.	+					
	20	9.6	9	9		+					
	25	10	-	-		+					
					(3)	0.75 (4)	0.19 (2)	0.06 (2)	0.0 (1)	(2)	(1)					

2	0	0	1	0	22.8	.	.	.	+	+	+	3	3	3	0	
	5	2	3	2		+	1	1	2		
	<u>10</u>	4.5	4	3		.	+	+	.	.	+	1	1	1		
	15	6.5	6	5.5		+	.	+	.	.	.					
	20	-	*	6		+	+	.	.	+						
					(2)	0.38 (3)	0.08 (2)	0.08 (2)	0.69 (4)	(1)	(1)					

3	0	0	0	0	12.4	.	+	+	.	.	+	3	3	3	1	
	5	1	3	0.5		+	+	+	.	.	.	3	1	2		
	10	2	3.5	1.2		+	+	+	.	.	.	2	1	2		
	15	3	4	2		+	+	+	.	+	.	1	1	1		
	20	3.5	4	4		+	+	+	.	.	.	1	1	1		
	25	4	-	-		+	1					
					(2)	0.94 (4)	0.25 (3)	0 (1)	0.13 (2)	(2)	(2)					

4	0	0.3	0.3	0.3	5.4	+	+	+	.	.	.	2	1	3	0	
	5	0.5	0.5	0.5		+	+	+	.	.	.	2	1	2		
	10	0.7	1	2		+	+	+	.	.	.	2	3	2		
	15	0.7	1.5	3		+	+	+	.	.	.	1	3	1		
	20	0.6	3	-		+	+	.	.	.	3	1				
	25	1	-	-		+	3					
					(1)	1.0 (4)	0 (1)	0 (1)	0 (1)	(2)	(1)					

5	0	1	1	1	30.7	.	.	.	+	.	+	3	3	2	2	
	5	3	3	2		+	+	1	2	2		
	<u>10</u>	6	5	4		+	+	1	2	2		
	15	-	8	7		+	.					
	20	-	-	-		+	.					
					(3)	0 (1)	0 (1)	0.36 (3)	0.82 (4)	(2)	(2)					

Site no.	Distance (m)	Depth (m)			Angle (degr.)	Soft bottom	Rubble	Broken rock	Bedrock	Cover avail.	Expo
6	0	1	1	1	34.0	+++	3 3 3	0
	<u>5</u>	2.7	2.5	1.5	 + .	+++	3 3 3	
	10	5.5	4.5	9	 +	+++		
	15	9	9	*	 +	. + .		
	20	-	11	-			
					(3)	0 (1)	0 (1)	0.23 (3)	0.77 (4)	(3)	(1)

7	0	1	1	0.5	22.0	. . +	. + .	+	3 2 3	0
	5	1.5	1	1		. + .	+ . + +	3 2 2	
	<u>10</u>	4.7	3	2.5		+ + .	+ +	1 1 1	
	15	8.8	6	5		+ + +	. . +		
	20	-	8.5	8		+		
25	-	11	11	+ .				
					(2)	0.5 (3)	0.31 (3)	0.06 (2)	0.19 (2)	(2)	(1)

8	0	1	1	1	37.5	+ + .	+++	3 3 1	2
	<u>5</u>	3.5	2.7	2.8		. . .	+ . +	1 1 1	
	10	6.5	6	6		. + .	+ . +		
	15	9.9	9	8.9		+ + .	+ + + +		
	20	13.5	12.2	11		. . .	+ +		
25	-	16	14	. .	+ +				
					(3)	0.18 (2)	0.65 (4)	0.12 (2)	0.24 (3)	(1)	(2)

9	0	0	0	0	36.5 + .	+ . .	+ . +	2 1 1	2
	<u>5</u>	3.8	1.7	2		. + +	. +	+ . +	1 2 2	
	10	8	5.3	5.7		+ + +		
	15	14.2	8	8.8		+ + .	. + +		
	20	-	9.8	12		+ +	+		
					(3)	0.57 (4)	0.29 (3)	0.07 (2)	0.43 (3)	(2)	(2)

10	0	0	0.5	1.2	24.6	. + .	. + .	+ . +	+ . +	1 3 3	2
	<u>5</u>	3.5	1.2	2.2		. + +	+ . +	1 3 1	
	10	9	3.1	4.4		. + +	+ . +		
	15	10.4	5	8		+ + +	. . .	+ +		
	20	-	6.6	9.3		+ +	. +	+ .	. .		
25	-	7	-	+ .	. .	+ .	. .				
					(3)	0.67 (4)	0.13 (2)	0.4 (3)	0.47 (3)	(2)	(2)

11	0	0	0	0	16.1	+++	3 3 3	3
	5	1.6	0.5	2.5	 +	+++	3 3 1	
	10	2.6	2.6	4		+ + +	. . + + .	1 1 1	
	15	4.1	4.2	5.5		+ + +	1 1 1	
	<u>20</u>	4.5	5	*		+ + +	1 1 1	
25	-	5.6	*	+ +				
						0.65	0.06	0.06	0.41		

Appendix 4

Site no.	Distance (m)	Depth (m)			Angle (degr.)	Soft bottom	Rubble	Broken rock	Bedrock	Cover avail.	Expo				
					(2)	(4)	(2)	(2)	(3)	(1)	(2)				
12	0	0	0	0	17.8	+	+	+	+	+	+	2	2	2	2
	5	1.5	1.5	1		+	+	+	+	+	+	1	1	3	
	10	4	3	4		+	+	+	+	+	+	1	3	1	
	<u>15</u>	5	4	*		+	+	+	+	+	+	1	1	1	
	20	5.6	6	*		+	+	+	+	+	+				
					(2)	1.00 (4)	0.27 (3)	0 (1)	0 (1)	(1)	(2)				
13	0	0	0	0	16	.	+	+	+	+	+	3	3	3	1
	5	1.5	1.5	1		.	+	+	+	+	+	1	2	2	
	10	3	3	2		.	+	+	+	+	+	2	3	3	
	<u>15</u>	4	4	4		.	+	+	+	+	+	1	1	1	
	20	*	*	6		.	+	+	+	+	+				
25	*	*	*	.	+	+	+	+	+						
					(2)	0.56 (4)	0.39 (3)	0 (1)	0 (1)	(2)	(2)				
14	0	0.5	1	0.5	15.4	.	.	.	+	+	+	3	3	2	2
	5	1.5	2.5	1		.	.	.	+	+	+	3	3	2	
	10	3	3.5	2		+	+	+	+	+	+	2	1	1	
	15	4	4.5	3		+	.	+	+	+	+	2	1	1	
	<u>20</u>	5	5	4		+	.	+	+	+	+	2	1	1	
25	6	-	5	+	+	+	+	+	+						
					(2)	0.53 (4)	0.24 (3)	0.47 (3)	0 (1)	(2)	(2)				
15	0	1	1.5	0.5	29.2	.	.	.	+	+	+	1	1	1	5
	5	3	2.5	2.5		+	+	+	+	+	+	1	3	3	
	<u>10</u>	6	3	5		+	+	+	+	+	+	1	3	1	
	15	8.5	6	8		+	+	+	+	+	+				
	20	-	9	10		+	+	+	+	+	+				
25	-	11.5	-	+	+	+	+	+	+						
					(3)	0.8 (4)	0.93 (4)	0 (1)	0 (1)	(1)	(2)				
16	0	0.5	1	0.5	18.7	.	.	.	+	+	+	2	3	3	7
	5	1.5	1	2		.	.	.	+	+	+	2	1	3	
	10	3	4.5	4		.	.	.	+	+	+	1	1	2	
	<u>15</u>	4	6	5		+	+	.	+	+	+	1	1	1	
	20	5.5	-	6		+	+	.	+	+	+				
25	*	-	7.5	+	+	.	+	+	+						
					(2)	0.4 (3)	0.07 (2)	0.13 (2)	0.6 (4)	(2)	(2)				
17	0	0.5	0.5	0	9.3	.	.	.	+	+	.	3	3	3	1
	5	1.5	1	2.5		+	+	+	+	+	+	3	3	3	
	10	1.5	1	2.5		+	+	+	+	+	+	3	3	3	
	15	2	1.5	3.5		+	+	+	+	+	+	1	3	3	
	20	2	-	4.5		+	+	+	+	+	+	1	1	1	

Site no.	Distance (m)	Depth (m)		Angle (degr.)	Soft bottom	Rubble	Broken rock	Bedrock	Cover avail.	Expo			
	25	2	-	-	+	+	.	.	1 2 1				
	30	-	2	-		+		+	1 1 1				
					0.75 (1)	0.31 (3)	0.06 (2)	0.19 (2)	(3)	(2)			

18	0	0.4	1	0.5	7.8	+	.	.	+	+	+	3 3 3	0
	5	0.4	2.5	1.5		+	+	.	+	+	+	3 1 2	
	10	0.4	3	2		+	+	.	.	+		3 1 1	
	15	1	4	2.5		+	+	.	.	.		3 1 1	
	20	1	*	3		+	+	.	.	.		3 1	
	25	1	-	-		+	.	.	+			3 1	
	30	1	-	-		+	.	.	.			3 1	
					0.82 (1)	0 (4)	0 (1)	0.47 (3)	(3)	(1)			

19	0	1	0.3	0	14.3	.	.	.	+	+	+	3 3 3	15
	5	0.5	2	1.8		.	.	.	+	.	+	2 3 3	
	10	1	2.5	4.3		+	.	.	.	+	+	3 3 3	
	15	2.5	3	6.6		+	.	.	.	+	+	3 3 3	
	<u>20</u>	2.8	4	7.7		.	+	.	.	+	+	2 3 3	
	25	5	5	9.3		.	+	.	.	+	+		
	30	3.2	7	-		+			
					0.2 (2)	0 (1)	0.05 (2)	0.75 (4)	(3)	(3)			

20	0	0.5	0.5	0.5	18.8	.	.	.	+	+	+	3 2 3	17
	5	2	1.5	2		.	.	.	+	+	+	3 1 3	
	10	3	2.5	2.5		.	.	.	+	+	+	3 3 3	
	<u>15</u>	7.5	4	3.5		.	.	.	+	+	+	3 3 3	
	20	9.5	5.5	4.5		+	.	.	+	+	+		
	25	10	6	8		+	.	.	+	+	+		
					0.17 (2)	0 (1)	0 (1)	1 (4)	(3)	(3)			

Appendix 5 - Macrophyte species recorded along each interval of three survey transects ([Dist] distance from shore). [+] present, [.] absent. Numbers refer to frequencies of occurrence with the associated variable levels in parentheses. Underlined distance indicates the 5 m depth boundary.

Site no.	Dist (m)	L.hyp	L.dig	L.sac	F.ser	F.ves	A.nod	H.sil	Z.mar
1	0	+	+	+	.
	5	+	+	+	.
	<u>10</u>	+	.
	15
	20
	25
		0 (1)	0 (1)	0 (1)	0 (1)	0.44 (3)	0.44 (3)	0 (1)	0 (1)

Appendix 5

Site no.	Dist (m)	L.hyp	L.dig	L.sac	F.ser	F.ves	A.nod	H.sil	Z.mar
2	0 + +	. + +
	5 +	+ . +	+ . +
	<u>10</u>
	15
	20 + +
		0 (1)	0 (1)	0.08 (2)	0.08 (2)	0.31 (3)	0.38 (3)	0 (1)	0 (1)

3	0 +
	5 +	+ . +
	10 +	+ . +
	15 +
	20
25	
		0 (1)	0 (1)	0 (1)	0.19 (2)	0.31 (3)	0 (1)	0 (1)	0 (1)

4	0	+ + +	. . +
	5	+ + +	. . +
	10	+ . + + +
	15	+ + +
	20	+	+ +
25	+	+ . .	
		0 (1)	0 (1)	0 (1)	0 (1)	0.73 (4)	0.13 (2)	0 (1)	0.47 (3)

5	0	+ + +	+ . +	+ + +
	5 +
	10
	15
	20
		0 (1)	0 (1)	0 (1)	0.36 (3)	0.18 (2)	0.27 (3)	0 (1)	0 (1)

6	0	+ . +	+ + +
	<u>5</u>	+ . +
	10 +
	15 + +
	20
		0 (1)	0 (1)	0.15 (2)	0.15 (2)	0.23 (3)	0 (1)	0 (1)	0 (1)

7	0	+ + +	+ + +
	5 + +	+ + +
	<u>10</u> +
	15
	20
25	
		0 (1)	0 (1)	0 (1)	0 (1)	0.38 (3)	0.38 (3)	0 (1)	0 (1)

8	0 + +	. + +

Site no.	Dist (m)	L.hyp	L.dig	L.sac	F.ser	F.ves	A.nod	H.sil	Z.mar
	<u>5</u>
	10
	15 + +
	20 + +
	25	+ +
		0 (1)	0 (1)	0.35 (3)	0 (1)	0.12 (2)	0.12 (2)	0 (1)	0 (1)

9	0	+ . +	. . +
	<u>5</u> + +	. + + + +
	10	+ + +
	15 + +
	20 +
		0 (1)	0 (1)	0.43 (3)	0.14 (2)	0.14 (2)	0.21 (3)	0 (1)	0 (1)

10	0 +	+ + +	+ + +	+ + +
	5 + +
	<u>10</u>
	15
	20
	25
		0 (1)	0 (1)	0.07 (2)	0.13 (2)	0.13 (2)	0.2 (2)	0 (1)	0 (1)

11	0 +	+ + +	+ + +
	5 + + +
	10 + +
	15
	<u>20</u>
	25
		0 (1)	0 (1)	0.12 (2)	0.18 (2)	0.06 (2)	0.18 (2)	0 (1)	0 (1)

12	0	+ + +
	5	+ . +
	10 + +
	<u>15</u> + +
	20 +
		0 (1)	0 (1)	0 (1)	0 (1)	0.47 (3)	0 (1)	0 (1)	0.2 (2)

13	0	+ + +	+ + +
	5 +	+ + +
	10 +	+ + +
	<u>15</u> + +
	20
		0 (1)	0 (1)	0.06 (2)	0 (1)	0.28 (3)	0.17 (2)	0 (1)	0.39 (3)

14	0	+ + +	+ + +	+ + +
	5 +	+ + +	. + +	+ + +	. . +	. . .

Appendix 5

Site no.	Dist (m)	L.hyp	L.dig	L.sac	F.ser	F.ves	A.nod	H.sil	Z.mar
	10	+ + +	+ . +	+ + +	. . .
	15	+ + +	. . + +
	<u>20</u>	+ + +	. . + +
	25	+ +
		0 (1)	0 (1)	0.71 (4)	0.59 (4)	0.29 (3)	0.35 (3)	0.24 (3)	0.12 (2)

15	0 +	+ + +	. + +
	5 +	. . +	. + +	. . +
	<u>10</u> + +	. . +	. . +
	15 + +	. . +	. . +
	20	+ +
	25	+
		0 (1)	0 (1)	0.53 (4)	0.27 (3)	0.47 (3)	0.2 (2)	0 (1)	0 (1)

16	0	+ + +	. . + +	. . .
	5	+ + + +
	10 +
	<u>15</u>	+ +	. .	. +
	20	. .	. +
		0 (1)	0.07 (2)	0.6 (4)	0.2 (2)	0.33 (3)	0.07 (2)	0.07 (2)	0 (1)

17	0	+ + +	+ + +
	5 + + +
	10 + + +
	15 + + + +
	20 +
	25 +	. .
	30 +	. .
		0 (1)	0 (1)	0 (1)	0.44 (3)	0.19 (2)	0.38 (3)	0.06 (2)	0.06 (2)

18	0 +	+ + +	+ + +
	5	+ . +	. . + +
	10 +	. . + +
	15 +
	20 +
	25 +	. +
	30 + +
		0 (1)	0 (1)	0 (1)	0.29 (3)	0.41 (3)	0.29 (3)	0 (1)	0.18 (2)

19	0	+ . +	. . +	. . .	+ . +	. . .
	5 + +	. + + + +	. . .
	10 +	. + + +	. + +	. . .
	15 + +	. + + + +	. . .
	<u>20</u>	. . + + +	. + + + +	. . .
	25	. + +
	30	. +	. .	. + +
		0.2 (2)	0 (1)	0.45 (3)	0.5 (3)	0.05 (2)	0.05 (2)	0.55 (4)	0 (1)

Site no.	Dist (m)	L.hyp	L.dig	L.sac	F.ser	F.ves	A.nod	H.sil	Z.mar
20	0	+ + +	. . +
	5	+ . + +	+ + +	. . .
	10	. . +	. . +	+ + +	. . .
	<u>15</u>	+ + +	. . +	. . +	+ + +	. . .
	20	. . +	. . +	+ + + +	. . .
	25	. . + + +	. . .
		0.44 (3)	0.17 (2)	0.22 (3)	0.22 (3)	0.06 (2)	0 (1)	0.61 (4)	0 (1)

Appendix 6 - Similarity matrix between the study sites based on the number of matching levels of the habitat variables.

1	1										
2	0.75	2									
3	0.64	0.70	3								
4	0.75	0.42	0.57	4							
5	0.70	0.57	0.57	0.57	5						
6	0.64	0.64	0.64	0.50	0.93	6					
7	0.85	0.80	0.75	0.64	0.64	0.57	7				
8	0.75	0.70	0.64	0.42	0.64	0.64	0.70	8			
9	0.75	0.64	0.70	0.50	0.75	0.75	0.70	0.75	9		
10	0.70	0.64	0.64	0.57	0.75	0.75	0.50	0.64	0.85	10	
11	0.64	0.80	0.75	0.50	0.57	0.64	0.57	0.70	0.80	0.89	
12	0.70	0.57	0.89	0.70	0.50	0.50	0.70	0.64	0.57	0.50	
13	0.75	0.64	0.70	0.85	0.42	0.33	0.75	0.50	0.57	0.64	
14	0.64	0.50	0.64	0.50	0.57	0.50	0.64	0.57	0.64	0.57	
15	0.70	0.57	0.75	0.64	0.64	0.57	0.50	0.80	0.64	0.70	
16	0.57	0.75	0.57	0.33	0.50	0.50	0.64	0.57	0.57	0.64	
17	0.57	0.42	0.64	0.50	0.64	0.64	0.64	0.50	0.70	0.50	
18	0.70	0.64	0.70	0.75	0.64	0.57	0.64	0.64	0.57	0.50	
19	0.33	0.50	0.33	0.33	0.57	0.57	0.42	0.42	0.50	0.42	
20	0.13	0.33	0.42	0.24	0.50	0.50	0.24	0.24	0.33	0.24	
11	11										
12	0.64	12									
13	0.64	0.80	13								
14	0.50	0.75	0.70	14							
15	0.70	0.75	0.70	0.64	15						
16	0.70	0.42	0.50	0.57	0.57	16					
17	0.57	0.64	0.42	0.64	0.50	0.42	17				
18	0.57	0.75	0.64	0.57	0.70	0.24	0.70	18			
19	0.57	0.24	0.33	0.24	0.42	0.64	0.50	0.33	19		
20	0.33	0.33	0.24	0.13	0.33	0.33	0.33	0.33	0.85	20	