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The trophic relationships of several commercial finfish species from the southwest Atlantic.

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This study aims to quantify the trophic relationships of seven commercially valuable predatory fish species (Argentine hake *Merluccius hubbsi*, southern hake *Merluccius australis*, Patagonian toothfish *Dissostichus eleginoides*, southern blue whiting *Micromesistius australis australis*, red cod *Salilota australis*, kingclip *Genypterus blacodes* and hoki *Macruronus magellanicus*) over a two-year period. A total of 1590 stomachs from these species was collected from the high seas of the southwest Atlantic and in the waters around the Falkland Islands. The percentage similarity index shows that all species except southern hake occupy very similar trophic positions, with a high percentage dietary overlap. Despite this, niche breadths were relatively narrow, with the majority of feeding occurring on locally abundant prey items (notothiniid fish and the squids *Illex argentinus* and *Loligo gahi*). In the two species for which sample size was largest, Argentine hake and kingclip, geographical differences in diet were found, which may be related to regional variation in prey abundance. The results are discussed in relation to the seasonal migrations of predators and prey and the hydroclimate regime.

Keywords: South West Atlantic, hakes, trophic interactions

1. Introduction

The South West Atlantic is a major fishing ground for several species of finfish and squid. Common hake (*Merluccius hubbsi*), Patagonian hake (*Merluccius australis*), toothfish (*Dissosticus eleganoides*) and the southern blue whiting (*Micromesistius australis australis*) are the main target species, with smaller catches of redcod (*Salilota australis*), kingclip (*Genypterus blacodes*) and Patagonian grenadier (also known as whiptail hake or hoki, *Macrouronus magellanicus*) being taken.

The trophic relationship between predatory fish and the trophic position of predatory fish in the South West Atlantic ecosystem are poorly understood, but are of great importance to fisheries management (Velasco & Olaso, 1998), in the context of which it is useful to understanding the patterns of resource use, intraspecific competition and the influence of predatory fish on the abundance and recruitment of other marine organisms (Du Buit, 1996).

The migratory behaviour of many commercial finfish and squid species in the South West Atlantic makes them vulnerable to both natural and man-made variations in prey availability. A decrease in prey availability in one area can thus result in a decrease in the predator fish population throughout its range. Due to the trans-boundary distribution of several species, stocks are also vulnerable to overfishing if stock assessments and management fail to account for fishing outside the area considered.

With the exception of *Merrlucius hubbsi*, relatively little is known about the biology of these species in the South West Atlantic although studies on hoki and kingclip in New Zealand waters and South African waters have been carried out (Mitchell, 1984; Clark, 1985). Studies on common hake mainly concern fish caught in Argentine and Uruguayan waters (Arena *et al.*, 1986; Otero *et al.*, 1986; Ubal *et al.*, 1987; Gaggiotti & Renzi, 1990; Prenske & Bezzi, 1991; Ruíz & Fondacaro, 1997). Data on the biology of commercial species found in Falklands waters are scarce (Norman, 1937; Wysokinski, 1974; Janusz, 1986; Arkhipkin *et al.*, 2001; Brickle *et al.*, 2001a,b; Mouat *et al.*, 2001).

The present study summarises results on stomach contents collected during 2000-2001 by observers working on the Spanish fleet fishing in the SW Atlantic.

2. Materials and Methods

Stomachs from seven different commercial species were collected by fisheries observers whilst on commercial fishing vessels and research vessels operating in the Southwest Atlantic during 2000 and 2001. Of the 1590 stomachs analysed, 1020 came from *Merluccius hubbsi*, 264 from *Genytrus blacodes*, 94 from *Dissostichus eleginoides*, 91 from *Macruronus magellanicus*, 80 from *Salilota australis* and 41 from *Micromesistius australis australis* (Table 1). For the majority of samples, biometric data on the fish (length, weight, sex and maturity) were also available. The samples were deep-frozen at Sea and shipped to Vigo (Spain), from where they were transported to Aberdeen (UK) for further analysis.

During stomach analysis the full stomach weight (FSW) was noted along with both empty stomach weight (ESW) and contents weight (CW). The fullness of the stomach and digestive state of each of the prey items was also noted. The contents were identified to the lowest level of classification possible.

In the case of cephalopod prey, length, weight, sex and maturity were noted whenever possible. If the cephalopod was too well-digested for identification or measurement, then lower beaks were retained. Body length was then estimated from measurement of lower rostral length (LRL) and application of published regression equations. Length and weight of fish prey were noted. For well-digested fish, generally the otoliths were retained and fish size estimated from otolith length, again with reference to published regressions. For *Sprattus fuegensis* (which has small and friable otoliths) the vertebral column length (VCL) was measured whenever possible. All other prey remains (generally invertebrates) were identified to class and then stored in 70% ethanol or frozen for later identification.

When prey items could not be identified further (e.g. due to absence of identifiable hard parts) they were assigned to one of five categories (Unidentified fish, Unidentified cephalopod, Unidentified crustacean, Unidentified mollusc and Miscellaneous invertebrate).

If a prey item was suspected to have been ingested whilst the fish was in the net (“net feeding”) then this was noted. Net feeding was suspected when the skin of the prey was in perfect condition and showed no signs of digestion. Suspected discard feeding was also noted, being identified when only certain parts of the prey body were ingested (e.g. the head

and or the remains of a filleted fish), where the prey was deemed too large to have been caught alive or when the stomach contents included items such as bacon and potatoes.

Importance indices for each prey category were calculated for each sampling area and for each size-class of predator (5cm or 10cm size classes depending on species, as well as overall values for each predator species. Sampling areas differed for each fish species depending on the fishing locations, but areas included: the High Seas around 42°S, High Seas around 46° and North, West and South of the Falkland Islands.

For each prey category, the indices of importance calculated were:

- (a) Percentage frequency of occurrence – the number of stomachs containing the prey category
- (b) Percentage by number – the estimated total number of individuals of the prey category in the set of stomachs as a percentage of the total number of all prey
- (c) Percentage by weight – the estimated total weight of the prey category in the set of stomachs as a percentage of the total weight of all prey
- (d) Index of Relative Importance (I.R.I) (Cortés, 1997).

Additionally, diets of different predator species were compared using the percentage similarity index (P.S.I) and Chi- squared analysis of frequency of occurrence data.

For the two predator species with highest numbers of samples (*M. hubbsi* and *G. blacodes*), the relationship between predator length and prey length was quantified using regression analysis.

3. Results and discussion

3.1. Southern Blue Whiting (*Micromesistius australis australis*)

In total 35 stomachs, collected from the area west of the Falkland Islands, contained prey remains (i.e. excluding discard and net feeding and empty stomachs). Crustaceans accounted for 92% of prey consumed, with euphausiid sp. being present in all stomachs and the

hyperliid amphipod, *Thermisto gaudichaudi* being found in 29% of the stomachs analysed (Fig. 1a). The remaining 8% of prey comprised unidentified fish (9% occurrence). No variation in diet in relation to fish length was found.

The results presented here are in agreement with previous studies on the diet of this species (Inada & Nakamura, 1975; Otero, 1977), which show it to be a pelagic feeder eating mainly pelagic invertebrates (euphausiids, Hyperliid amphipods) and some small fish. Copepods and small cephalopods were found in diet in Argentine waters but not recorded in this study – although our sample size was rather small. Studies in New Zealand (Clark, 1985) also indicate feeding on pelagic invertebrates, with the diet comprising of amphipods and the Decapod suborder Natantia. Sample size was insufficient to detect any ontogenetic variation in diet.

3.2. Hoki (*Macruronus magellanicus*)

Overall, 72 stomachs of hoki containing food remains were collected from areas north and west of the Falkland Islands and at 42°S. Crustaceans were the most important prey category, accounting for 55% of the prey consumed, comprising mainly euphausiids (occurring in 45% of stomachs) and *T. gaudichaudi* (20% of stomachs). Fish occurred in 31% of the stomachs analysed. Cephalopods were also found in the diet. In terms of biomass, fish formed the bulk of the diet (83%), with nototheniid sp. and Falkland herring (*Sprattus fuegensis*) contributing most to this total.

The hoki sampled ranged in size from 12-46cm pre-anal length (PAL). In fish less than 20cm PAL, euphausiids dominated the diet. In fish above 20cm PAL, the diet consisted mainly of fish. In areas 1 and 2, the diet was dominated by euphausiids, while in area 3 fish dominated the diet. However, it should be noted that this may largely be a consequence of the hoki caught in area 3 being generally bigger than those caught in areas 1 and 2.

Hoki are known to undergo vertical migrations, ascending in the evening to the midwater regions and returning at dawn to the sea bottom (Kerstan & Sahrhage, 1980). Feeding in hoki has been related to the vertical migration of the hyperliid amphipod, *T. gaudichaudi* (Sánchez, 1999), one of the main crustacean prey found in the present study. The euphausiid,

fish (*Sprattus fuegensis*) and myctophid prey found in the stomachs of hoki are all found at the surface and in midwater, consistent with hoki feeding predominantly in the pelagic zone. Previous studies on both hoki and related species (*Macruronus novaezelandiae*) confirm the conclusion that they are mainly pelagic feeders (Clark, 1985; Sánchez, 1999).

Notothenids, especially *Patagonotothen ramsayi* are highly abundant in the waters around the Falkland Islands and are important components in the diet of many marine predators in this area (Arkhipkin *et al.*, 2001; Brickle *et al.*, 2001a,b). One noticeable absence amongst the prey items recorded in the present study was juvenile southern blue whiting, which has been reported as being the most important prey item of post-spawning hoki in the waters around the Falkland Islands (Janusz, 1986). Seasonal changes in the diet of hoki is one possible explanation for this discrepancy - seasonal variation was not examined in this study due to small sample size.

This study generally confirms previous work on ontogenetic variation in hoki diet, with pelagic crustaceans being the most important prey of small fish and a shift toward fish prey in larger individuals (Clark, 1985; Sánchez, 1999). The shift in diet occurs at around 26-30cm PAL, the smallest size class in which the weight of fish in the stomachs exceeded the weight of crustaceans. The fact that some crustaceans are found in the diet of larger fish indicates that this not a active change in diet but is due to a wider range of prey becoming available to the fish. Larger fish are generally able to catch and consume larger prey items (Clark, 1985). The results suggest that hoki are opportunist feeders rather than specialist feeders, with more types of prey becoming available to the fish as it grows larger.

3.3. Redcod (*Salilota australis*)

In total 74 stomachs containing prey remains were collected from areas north and west of the Falkland Islands. Twenty-two different types of prey were identified in the stomachs, with crustaceans being the most important. Benthic isopods were the most frequently recorded crustacean prey, occurring in 66.22% of stomachs, although representing only 7% of the total weight of prey consumed. Benthic amphipods were the second most frequent prey item, occurring in 49% of stomachs but representing only 2% of the diet by weight. Other

important crustaceans included unidentified decapods, (20% occurrence) and the benthic amphipod *Sirolus* sp. (12% occurrence).

Fish were found in 27% of stomachs, of which *Patagonotothen ramsayi* was the most frequently identified and also the most important prey in terms of biomass (68% of the diet). Other prey items found included echinoderms, the decapod *Peltarion spinulosm*, cephalopods and polychaetes.

Stomachs analysed were from fish ranging in size from 31-78cm total length (TL). In fish less than 45cm TL, crustacean prey (mainly benthic isopods) dominate the diet. At larger sizes, notothenids replace crustaceans as the dominate prey item, with the proportion of notothenids in the diet remaining fairly consistent (0.68 – 0.79) in all larger size classes from 46cm. The importance of cephalopods in the diet increases in larger fish. In area 2, cephalopods predominated in the diet (in terms of biomass) whereas in areas 1 and 3 nototheniid prey made up the bulk of prey by weight.

The results presented here are in general agreement with previous work (Perez Comas, 1980; Arkhipkin *et al.*, 2001) in that the diet of small fish consisted mainly of crustaceans while in larger fish it consisted mainly of fish. As found by Arkhipkin *et al.* (2001), redcod were seen to be near-bottom feeders, preying on benthic amphipods and notothenid fish.

It is notable that pelagic crustaceans constituted up to 60% of prey taken on the Patagonian shelf (Perez Comas, 1980) but were not recorded in the diet in this study or by Arkhipkin *et al.* (2001). This may reflect differences in prey abundance or a real geographic shift in feeding strategy by redcod.

Arkhipkin *et al.* (2001) showed the squid *Loligo gahi* to be the main prey item of redcod during July-October around the Falkland Islands, when *L. gahi* is found in deeper water. Notothenid fish are found all year round in the Falkland Islands and represent an abundant source of prey throughout the year for most predatory fish including redcod (Arkhipkin *et al.*, 2001). Due to the small sample size seasonal variation in diet was not examined in the present study, although Arkhipkin *et al.*, (2001) found that redcod diet varies depending on local abundance of prey throughout the year.

3.4. Toothfish (*Dissostichus eleginoides*)

Seventy-three non-empty stomachs of toothfish were collected from areas to the south and west of the Falkland Islands and at 44° South on the high seas. Fifteen different types of prey were identified in the stomachs, with fish the most important prey category (occurring in 57% of stomachs).

Unidentified fish were frequent (37% occurrence) and made a significant proportion of prey weight (287%). Of species that could be identified, notothenids were found in 16% of stomachs (25% of prey by weight), of which *P. ramsyii* occurred in 9% of stomachs (13% of prey by weight). Cephalopods occurred in 33% of stomachs with *Loligo gahi* being the most prevalent, occurring in 16% of stomachs (9% of prey by weight). Other cephalopod prey included *Illex argentinius* and *Semirossia patagonica*.

Stomachs were analysed for fish ranging in size from 29-79cm TL. In fish less than 50cm TL, the dominant prey were cephalopods, mainly *Loligo gahi* (75%). In larger sizes the importance of squid was reduced and fish, especially notothenids, became the predominant prey. Redcod made up significant percentage of the diet of fish in the 66-70cm size class (24%). There was a marked difference between samples from the south of the Falkland Islands and samples from the north and west of the Falkland Islands. The data from the south of the Falkland Islands shows that *L. gahi* is the most important prey item, constituting over 90% of the prey taken by weight. In contrast the prey taken to the north and west of the Falkland Islands was mainly fish, with the notothenids (especially *P. ramsyii*) being the most important prey item by weight. It is apparent however that the ontogenetic and geographic differences in diet are difficult to separate given a small sample size.

Little is known about the biology of the Patagonian toothfish. Juveniles are known to inhabit shallow waters in the shelf region, with fish migrating down the slope with increasing size. Adult fish are found at depths of 1000m or more, where a directed fishery exists. Studies on Patagonian toothfish in Argentinean waters have shown that the diet consists of crustaceans, cephalopods and fish (Cassia & Perrotta, 1996). An ontogenetic shift in diet is observed with small fish found in shallow waters feeding primarily on crustacean prey and large fish feeding primarily on fish (Cassia & Perrotta, 1996). A similar observation was made in this

study with toothfish shifting from a diet of predominantly cephalopods to one that mainly consists of fish. Feeding on cephalopods was observed mainly to the south of the Falkland Islands, where the squid *L. gahi* is highly abundant (Rodhouse, 1995), whereas to the north and west of the Falkland Islands the prey consisted mainly of notothenids, again highly abundant species on the Patagonian shelf. It can be suggested that toothfish found in Falkland waters are responding to the availability of prey species rather than feeding selectively, due to the high abundance of the two main prey items in the areas studied.

3.5. Kingclip (*Genypterus blacodes*).

In total 208 stomachs containing food remains were collected from areas west and north of the Falkland Islands and at 44°-46° south on the high seas. Thirty-two different prey categories were identified, with fish found to be the most important prey item (56% occurrence). The most commonly occurring fish were unidentified notothenids (26% occurrence) and *Patagonotothen ramsyii* (26% occurrence), with the eelpout *Iluocetes fimbriatus* being the next most important fish prey item (4% occurrence). *P. ramsyii* was the most important prey item in terms of biomass (32% of the total prey weight), followed by unidentified notothenids (25%) and *Macruronus magellanicus* (6%).

Crustaceans were the second most important broad category of prey category (29% occurrence). The most commonly occurring crustaceans were benthic isopods (32% occurrence, although these contributed only 2% of prey biomass). The benthic isopod, *Serolis* sp. and unidentified shrimps were also important components of the crustacean diet both occurring in 7% of stomachs, but each only accounting for less than 1% of prey biomass.

Cephalopods, other molluscs and miscellaneous prey were of minor importance in the diet of kingclip, occurring in only 15% of stomachs and making up 15% of the total weight of prey consumed.

Stomachs analysed were from fish ranging in size from 16- 128cm total length. Fish dominated the diet for all length classes, although the importance (by weight) of fish prey increased with fish length. In kingclip <20cm TL, fish accounted for just over half the prey consumed, while in kingclip over 80cm TL, fish made up over 95% of prey consumed.

Benthic isopods were taken only by fish of <50cm TL, and the only other occurrence of benthic invertebrates was in the diet of the 61-70cm TL size class. Cephalopod prey were found only in fish of 31-50cm TL.

The size of fish prey eaten by kingclip was significantly correlated with (kingclip) fish length ($R=0.456$, $N=118$).

There was little variation in the diet between fish from the three studied areas (High Seas above 47°S, North Falkland Islands and West Falkland Islands). However, skates (*Bathyraja albomaculata* and *Bathyraja brachyrops*) were found in stomachs from fish around the Falkland Islands whereas hake was only found in stomachs from fish on the high seas above 47°S.

The results of this study, and of other studies on related species, suggest that kingclip is a benthic feeder (Mitchell, 1984; Clark, 1985), with benthic amphipods and benthic notothenids (especially *P. ramasyii*) being the dominant prey items. This differs from observations on *G. blacodes* diet in New Zealand waters, where *Macruronus novaezelandiae* and *Munida gregaria* were the main prey species (Mitchell, 1984). This difference is of interest as *M. magellanicus* is a close relative of *M. novaezelandiae* and *Munida gregaria* are abundant in Patagonian shelf waters (AB pers. obs.).

As with most other the other predator fish species studied, ontogenetic changes in the diet were observed, with many crustaceans in the diet of smaller fish while larger individuals fed almost exclusively on fish. An ontogenetic shift in diet from crustaceans to fish was observed *G. blacodes* in Argentinean waters and in *G. blacodes* in New Zealand waters (Mitchell, 1984; Clark, 1985).

The lack of pelagic crustaceans in the diet of kingclip suggests that kingclip does not undergo the vertical migrations iseen in other fish and cephalopod predators (Kerstan & Sahrhage, 1980; Sánchez 1999; Mouat *et al.*, 2001) in the southwest Atlantic, preferring to remain on or close to the bottom whilst feeding. This reliance on benthic organisms as prey was also observed in *G. blacodes* in Argentinean waters. The preference for benthic prey is emphasised by the presence of other benthic organisms in the diet such as echinoderms, asteroidea, Rajiidae and the scallop, *Chalmys patagonica*.

The presence of notothenid prey in the diet of all size classes of kingclip indicates its importance as a food item. Whether kingclip are specialist feeders which actively target notothenids or whether they are opportunistic predators feeding off the most abundant prey type is unknown but the presence of other benthic organisms in the diet of kingclip, especially the large ones, tends to suggest that kingclip are opportunistic feeders.

3.6. Common hake (*Merluccius hubbsi*)

Hake stomachs were collected from most areas of the southwest Atlantic in the high seas and waters around the Falkland Islands (39°S – 54°S). Overall, 895 non-empty stomachs yielded 34 different categories of prey. Cephalopods were the most important prey category occurring in 41% of the stomachs. The Patagonian squid, *Loligo gahi* was the most important cephalopod prey species (32% occurrence, 28% of prey biomass). Other cephalopods eaten included Argentine short finned squid, *Illex argentinus* (5% occurrence, 1% biomass) and unidentified cephalopods (13% occurrence, 4% biomass).

Fish were the second most important broad prey category, occurring in 29% of stomachs, while crustaceans occurred in 27% of stomachs. The most important fish prey species was the notothenid, *P. ramsyii*. Although only occurring in 9% of stomachs it was the most important prey item consumed by weight (34% biomass). The Falkland herring, *S. fuegensis*, occurred in 8% of stomachs and made up 9% of the total weight of prey consumed. Probable cannibalism was observed, with *Merluccius* sp. found in 1% of stomachs and making up 1% of the total weight of prey taken. Amphipods (14% occurrence) and euphausiids (9% occurrence) were the most important crustacean prey, although neither made up more than 1% of prey biomass.

Stomachs analysed were from fish ranging from 18-98cm total length. Cephalopods predominated in the diet of hake upto around 50cm TL after which fish became more important. In the smallest hake (<30 cm TL), Argentine short finned squid, *I. argentinus* made up 70% of the weight of prey consumed. In fish of 31-70cm *L. gahi* predominated. No *I. argentinus* was found in stomachs of hake over 70cm in length. At 50cm *S. fuegensis* begin to appear in the diet, and reached peak importance in hake of 51-55cm TL. In the

largest fish, notothenids dominated the diet. The size of individual *Loligo*, *Illex* and notothenids taken by hake increased with hake body length ($R=0.159$, $N=387$; $R=0.527$, $N=73$; $R=0.677$, $N=93$ respectively).

There were marked differences in the prey taken between the different areas (high seas above 40°S, high seas above 46°S, North/west of the Falkland Islands and south of the Falkland Islands). Above 40°S, the main prey was *I. argentinus* with small amounts of the clupeid *Engraulis anchoita* present. Above 46°S the diet was more diverse with *I. argentinus* less predominant in the diet and notothenids being the most important prey type by weight. Cannibalism on juvenile hake was also seen at 46°S. Notothenids formed the bulk of the diet north/ west of the Falkland Islands, with *L. gahi* being the main cephalopod species eaten. In the area south of the Falkland Islands, *L. gahi* was the most prominent prey item and notothenids were unimportant.

At least two stocks of common hake are thought to exist in the southwest Atlantic, both of which undergo seasonal cyclical migrations. The northern stock migrates along the shelfbreak between the coast of Uruguay (35°S) and the coast of Argentina (45°S) while the southern stock migrates between the latitudes of 44°S and 53°S (Otero & Kawai, 1981; Ubal *et al.*, 1987).

The diet of common hake is known to vary along its migratory route, resulting in latitude-related and seasonal variation in diet (Stott, 1982; Ciechomski & Sánchez, 1983; Ubal, 1986; Ubal *et al.*, 1987; Podestá, 1989; Prenske & Bezzi, 1991; Haimovici *et al.*, 1994; Ruíz & Fondacaro, 1997).

The northern stock of common hake is closely associated with the Brazil/ Falklands confluence (Podestá, 1989). The shelfbreak between the Falklands current and the South American continental shelf is an area of high productivity, with the high productivity in spring/summer due to the high concentrations of phytoplankton. This high productivity does however decrease rapidly after the spring/summer bloom. The high concentration of zooplankton provides food for pelagic fish and cephalopod species, which in turn provide food for species from higher trophic levels such as hake, which accumulate along the shelf front (Podestá, 1989). The distribution of *E. anchoita*, which is an important prey item for hake found in northern waters is closely associated with the shelfbreak (Brandhorst *et al.*,

1971). Both the common hake and *E. anchoita* migrate offshore and northwards along the slope in autumn following the decline in the zooplankton biomass, with the hake feeding actively on *E. anchoita* as they migrate (Ciechomski & Sánchez, 1983). *I. argentinus* is also an important prey item in late autumn/winter, when dense concentrations occur along the shelfbreak, and it found in increasing numbers in the stomachs of hake between April and July (Cordo, 1981).

The importance of *I. argentinus* and *E. anchoita* in the stomachs of hake from this study in the high seas above 40°S is consistent with these fish belonging to the northern spawning stock, which is known to migrate offshore along with *E. anchoita* as they migrate northwards to their spawning grounds (Podestá, 1989). The dietary data from this study are consistent with previous studies on hake feeding within the Argentine/ Uruguayan common fishing zone between 35°S and 45°S (Ciechomski & Sánchez, 1983; Ubal, 1986; Podestá, 1989; Prenski & Bezzi, 1991; Ruíz & Fondacaro, 1997).

The diet of common hake from the southern stock is less well understood. Stott (1982) indicated that the diet of hake in Falkland waters consisted mainly of southern blue whiting, *Notothenia* spp. and the remains of small squid. This study reveals that the diet of hake in Falkland waters is dominated by the Patagonian squid *Loligo gahi* south of the Islands, and by *Notothenia* spp. to the north and west of the Islands.

Nototheniids are common on the Patagonian shelf south of 35° and are highly abundant in the waters around the Falkland Islands (Laptikhovskiy & Arkhipkin, In Press), where large by-catches from the multinational fishery occur - resulting in large numbers of discards. *L. gahi* is also abundant around the Falkland Islands, where a multi-national fleet fishes for it during two seasons. The majority of the fishing occurs to the south and east of the Falkland Islands shelf edge where *L. gahi* is most abundant (Rodhouse, 1995). Spawning of *L. gahi* occurs in shallow waters with the squid migrating into deeper waters as they mature (Rodhouse, 1995).

The prevalence of *L. gahi* and notothenids in the diet of common hake in Falkland waters would indicate that common hake found in here are feeding on the most abundant food sources available. As with common hake from the northern stock it can be suggested that common hake undergo their southward migration to find an adequate source of food for maintenance, growth and reproduction (Podestá, 1989), migrating northward again to return

to suitable spawning grounds off the Argentinean coast. As with the waters associated with the Brazil/Falklands confluence, the waters around the Falkland Islands are highly productive due to cold waters from the Antarctic circumpolar current moving northwards along the Patagonian shelf (Strange, 1992). The data reported here suggest that the southern stock of common hake migrates southwards along with *I. argentinus*, the hake feeding actively on *I. argentinus* as they migrate. *I. argentinus* grow as they migrate southwards during the autumn along the Patagonian shelf where they feed pelagic crustaceans (Mouat *et al.*, 2001). The relatively small size of *I. argentinus* taken by common hake in this study would also suggest that *I. argentinus* become too large to be an energetically viable source of prey (more energy expended in catching than gained from eating). Growth in *I. argentinus* is rapid and by the time *I. argentinus* reach the Falklands (20-23cm) they are too big for hake to catch, thus resulting in a switch to more easily caught abundant prey such as notothenids and loliginids.

As with all other species of hake, the feeding of *M. hubbsi* seems to be intrinsically linked to a productive upwelling system, in this case the Brazil/Falklands confluence and the Patagonian shelfbreak. Due to this there is a heavy reliance on the abundant cephalopod and fish prey found in these areas that are also targeted for commercial purposes (Podestá, 1989; Lipinski *et al.*, 1992; Haimovici *et al.*, 1994; Du Buit, 1996). In the case of the Southern stock of *M. hubbsi* there is a reliance on the abundant cephalopod species found along the Patagonian shelf, both of which are targeted by directed fisheries. The Northern stock also relies on abundant species (*I. argentinus* and *E. anchoita*) that are subjects of directed fisheries. It has been shown in *Merluccius merluccius* that 95% of its potential food is also fished for commercial purposes (Du Buit, 1996).

The diet of most of the studied fish species shows a high level of overlap (Table 2).

4. General discussion

4.1. Predation on commercial species.

Southern blue whiting was found in small quantities in the diet of common hake, Patagonian hake, toothfish and redcod. It has been shown to be a major component in the diet of Patagonian hake *Merluccius australis* from Southern Chile (Paya, 1992), comprising up to

30% of the total diet by weight, with similar amounts being taken by all size classes. In common hake from Falkland waters, southern blue whiting was also found to be a major dietary component in the Northeast region (Stott, 1982) although no figures were given. Juvenile southern blue whiting was reported to be a major component in the diet of hoki (Janusz, 1986), although more recent studies (A. Taylor, unpublished) have shown that they make up only a small fraction of the diet. These contrasting figures suggest that hoki simply eats southern blue whiting when it is available.

Southern blue whiting is also a major component of the diet of *G. blacodes* in New Zealand waters where, along with *M. novaezelandiae*, it is taken during the day whilst southern blue whiting is near the sea bottom (Clark, 1985). Feeding on southern blue whiting by *G. blacodes* in New Zealand waters is however seasonal, with southern blue whiting taken whilst spawning, which increases their vulnerability to predation (Clark, 1985).

Hoki was found in small quantities in the diet of common hake and kingclip, but constituted the main part of the diet of the Patagonian hake. Hoki are known to be a major component of prey taken by Patagonian hake in southern Chile and make up over 60% of the total weight of prey consumed by larger hake (Paya, 1992). Kingclip in New Zealand waters feed on the similar *M. novaezelandiae*, the hoki being taken during the day time whilst they are on or near the sea bottom (Clark, 1985).

Predation on **common hake**, although limited to a few individuals in *G. blacodes* and *M. hubbsi* in this study can be extensive. *Illex argentinus* (Santos & Haimovici, 1997), *Squalus acanthius* (García de la Rosa & Sánchez, 1997), dusky dolphins *Lagenorhynchus obscurus* (Alonso *et al.*, 1998) have all been shown to prey on common hake at varying stages of their life cycle.

Cannibalism in hake species is not uncommon (Prenski & Bezzi, 1991; Lipinski *et al.*, 1992; Ware, 1992; Du Buit, 1996; Ruíz & Fondacaro, 1997; Velasco & Olasso, 1998), but does vary between species. Cannibalism in *M. hubbsi* seems to be almost exclusive to common hake feeding in and around the nursery grounds. In the northern nursery grounds, the most intense cannibalism takes place each autumn with 70,000 tonnes estimated to be taken (Prenski & Benzzi, 1991). However in the spawning grounds for the northern stock, the rate of

cannibalism is lower due to the abundance of the white shrimp *Peisos petrunkevitchi* which makes up 79% of diet in spawning grounds (Ruíz & Fondacaro, 1997).

In South African coastal waters, cannibalism accounts for 20% of the annual ration of cape hakes (*M. capensis* & *M. paradoxus*) (Payne *et al.*, 1987). Cannibalism in *M. capensis* is seasonal and an estimated 500,000 tonnes removed annually through cannibalism (Payne *et al.*, 1987). In the European hake, *M. merluccius* there is limited cannibalism (Du Buit, 1996), due to the segregation of adults and juveniles by area.

Cannibalism in *M. hubbsi* seems to be related to the abundance of alternative prey items, such as *P. petrunkevitchi* in the spawning grounds (Ruíz & Fondacaro, 1997), but also the segregation of adults from juveniles for the majority of the year, as juvenile *M. hubbsi* do not undertake the seasonal migrations along with the adults (Angelescu & Prenske, 1987).

4.2. Conclusions

Ontogenetic changes in diet, as here reported for most of the studied species, are thought to help regulate the competition between juveniles and adults for food (Ubal, 1986). The differences in diet between areas (although not always easy to disentangle from ontogenetic changes) show that predatory fish tend to feed on locally abundant prey items, with heavy reliance on a few species, such as notothenid fish and the squids *L. gahi* and *I. argentinus*.

The cyclical migratory behaviour of many of the prey species either along the Patagonian shelf (such as *E. anchoita*, *S. fuegensis*, *I. argentinus*) or by depth (*L. gahi*, *M. ingens*) has resulted in the non-migratory and abundant notothenid fish being the dominant prey item for all species studied bar southern blue whiting. Migratory species occur in the diet only when they become locally abundant and available to the predator. This results in predatory fish having narrow niche breadth ranges but with a few prey species having a high index of relative importance.

The impact of predation on the high seas and around the Falkland Islands is limited due to the fact that most predation mortality occurs in fish of a young age. Immature fish tend to be found in shallow waters along the Patagonian shelf away from the areas targeted by the

commercial fishing vessels used in this study. Direct predatory interactions between the study species in the study area appeared to be relatively important, although increased predation on southern blue whiting is to be expected during the spawning season (as seen for the predation on southern blue whiting by *G. blacodes* in New Zealand waters).

A high level of dietary overlap seems to exist between different commercial fish species in the southwest Atlantic, as a result of the dependency on few prey species. However, a full picture of trophic relationships will require data from all seasons.

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Table 1. Summary of stomachs sampled

Key: HAK = Common hake (*Merluccius hubbsi*), KIN = kingclip (*Genypterus blacodes*), TOO = toothfish (*Dissosticus eleganoides*), HOK = hoki (*Macruronus magellanicus*) BLU = southern blue whiting (*Micromesistius australis australis*), RED = redcod (*Salilota australis*).

| Numbers | HAK | KIN | TOO | HOK | BLU | RED |
|--------------------------------|------------|------------|------------|------------|------------|------------|
| Stomachs analysed | 1020 | 264 | 94 | 91 | 41 | 80 |
| Net feeding | 53 | 2 | 2 | 0 | 0 | 0 |
| Discard feeding | 78 | 17 | 19 | 0 | 0 | 5 |
| Empty stomachs | 42 | 47 | 9 | 19 | 6 | 5 |
| Stomachs with prey | 895 | 208 | 73 | 72 | 35 | 74 |
| Prey categories present (mean) | 1.06 | 1.44 | 1.23 | 1.22 | 1.03 | 1.72 |

Table 2. Diet overlap in the studied species: Percentage Similarity Index values.

| | | | | |
|------------------------|---------------------|-----------------------|--------------------|------------------|
| | <i>S. australis</i> | <i>D. eleginoides</i> | <i>G. blacodes</i> | <i>M. hubbsi</i> |
| <i>M. magellanicus</i> | 9.44 | 50.25 | 47.78 | 23.87 |
| <i>S. australis</i> | | 25.95 | 42.15 | 46.56 |
| <i>D. eleginoides</i> | | | 70.28 | 42.54 |
| <i>G. blacodes</i> | | | | 48.07 |