Although organisms from all phyla and all marine habitats consume dead carriion, trophic transfer of scavenged material, and processes associated with this transfer, are poorly understood (Britton & Morton 1994). The death of mobile consumers (such as fish and whales) leads to nutrient and energy transfer across ecosystem boundaries (Payne & Moore 2006) and substantial carriion subsidies can increase secondary pro-

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**Introduction**

N. J. King¹,*, D. M. Bailey², I. G. Priede¹

¹Oceanlab, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, UK
²University of Glasgow, Institute of Biomedical and Life Sciences, Graham Kerr Building, Glasgow G12 8QQ, UK

Although organisms from all phyla and all marine habitats consume dead carriion, trophic transfer of scavenged material, and processes associated with this transfer, are poorly understood (Britton & Morton 1994). The death of mobile consumers (such as fish and whales) leads to nutrient and energy transfer across ecosystem boundaries (Payne & Moore 2006) and substantial carriion subsidies can increase secondary pro-

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Email: n.king@abdn.ac.uk

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baited cameras, across a wide range of disciplines (coral reef management, deep-sea biology, neurobiology, hydrodynamics, and forensic science). In this Theme Section (TS) we intend to advance the field of marine scavenger biology by bringing together current expertise to discuss future research avenues, encourage collaboration, identify research areas in need of additional attention, compare techniques, and essentially spark debate.

**Baited cameras.** Marine scavengers are defined by Britton & Morton (1994) as organisms which are ‘able to detect carrion, usually by either distance or touch chemoreception, or both, deliberating to move toward it, and eventually consume either part or all of it’. The exploitation of this behaviour has enabled fishers and scientists to use bait to harvest marine scavengers, and to obtain information on behaviour, densities, distribution and life history. Baited cameras use bait to attract organisms into the field of view where still images or video can be recorded at pre-set intervals. Baited cameras have been used to assess marine biodiversity and organism abundance, particularly in the deep-ocean, since the late 1960s (Bailey et al. 2007, this TS), but are now increasingly used in shallow water habitats, such as Marine Protected Areas, for more applied purposes such as fisheries assessment and biodiversity surveys (Ellis & Demartini 1995, Cappo et al. 2004, Morrison & Carbines 2006, Watson et al. 2007). Malcolm et al. (2007, this TS) present a wide-scale baited video camera survey of spatial differences and temporal changes in the diversity of temperate reef-fish assemblages from 3 marine parks over 5 years. Fish assemblages were found to vary within and between marine parks, with time playing a less important role than spatial separation in structuring fish assemblages. Malcolm et al. (2007) concluded that a network of marine parks is therefore required to allow for the spatial variation in the fish assemblages observed. Cappo et al. (2007, this TS) identified spatially separated vertebrate communities in lagoon and inter-reef waters of the Great Barrier Reef Marine Park, Australia. The study extended over 14° of latitude and the entire shelf, and identified 347 species of osteichthyans, chondrichthyans, and sea snakes. Nine vertebrate communities, made up of 17 spatially adjacent groups were identified, with community boundaries strongly correlated with oceanography and habitat type. Harvey et al. (2007, this TS) found that baited camera systems (compared to unbaited) had less variability when replicated, allowing greater statistical power to discriminate spatially distributed temperate and tropical shallow fish assemblages. In addition, the baited cameras were found to attract increased numbers of predatory and scavenging species, without decreasing the number of other trophic groups present, such as omnivorous and herbivorous fish species. Shallow baited-camera studies in pelagic habitats are rare; however, Heagney et al. (2007, this TS) have used mid-water baited video to assess pelagic fish assemblages off the east coast of Australia. In agreement with the benthic baited camera studies Heagney et al. (2007) have also found regional fish communities, with current speed having the greatest influence on assemblage structure.

The main advantages of baited camera systems are that they are non-destructive, photograph organisms in situ and are extremely efficient in their use of ship-time, i.e. they are generally autonomous, independent of the vessel and can be pre-programmed and left on the seabed. However, as with any sampling method, there are biases associated with baited cameras. The contribution by Bailey et al. (2007) introduces and reviews the advantages and use of baited cameras in deep-water environments, outlining sampling biases, and highlighting how baited camera-derived data compare with data obtained using other survey methods. Robust and realistic models are needed to predict local abundances of scavengers attracted to baited cameras, with most of the work to date being focused on the abyssal grenadier, *Coryphaenoides armatus* (Hector, 1875). Farnsworth et al. (2007, this TS) assess baited camera abundance-estimating techniques and provide an alternative stochastic model allowing quantification of the precision of such abundance estimates for *C. armatus*. As well as sampling bias and the currently limited abundance-estimate models, baited cameras can also be obtrusive and can produce artefacts within the data obtained (Jamieson et al. 2006). Raymond & Widder (2007, this TS) demonstrate that the spectral quality (white, red and far-red) of the light used to illuminate video sequences can affect the behaviour of the sablefish *Anoplopoma fimbria* (Pallas, 1814) more than another species, the pacific grenadier *C. acrolepis* (Bean, 1884) at a baited camera. Interestingly, the differences in behaviour between the 2 species are attributed to the differences in retinal spectral sensitivity associated with differences in life histories.

**Anthropogenic impacts on scavengers.** Scavenger ecology is also relevant to the understanding of anthropogenic impacts on the oceans. In particular, recent research has revealed the positive effect of fishery discards on seabird and marine benthic scavenger populations (e.g. Camphuysen et al. 1995, Garthe et al. 1996, Catchpole et al. 2006). It is estimated that a biomass equivalent to approximately 27% of global fish catches (Alverson et al. 1994) is discarded by fishery fleets and that seabirds consume 50% of that discarded material (Jennings & Kaiser 1998). However, surface-feeding seabirds are selec-
tive in the items they consume which can directly affect the type and supply of offal available to benthic scavengers on the sea floor below (Furness et al. 2007, this TS). Debate continues as to whether benthic scavenger populations mirror the observed increases in seabird populations, and it has been suggested that fisheries discards can only sustain benthic carnivores for approximately 3 d yr⁻¹ (Kaiser & Hiddink 2007, this TS). The anthropogenic impact of fisheries is, however, no longer the only risk to the marine environment. Increased carbon dioxide within our atmosphere has the potential to alter the chemistry of the oceans, and there are prospective plans to store excess carbon dioxide in the deep ocean. To address this issue Barry & Drazen (2007, this TS) studied the reaction of several caged deep-sea scavengers to episodic flushes with CO₂ rich water. The survival of caged marine scavengers varied, but interestingly all Coryphaenoides armatus perished, potentially as a result of cage-related stress. Macrourids are a dominant abyssal scavenger and a lack of tolerance to stresses that will accompany expected future changes in ocean chemistry are of major concern.

The way forward. This TS on the role of scavengers in marine ecosystems has brought authors from several fields of scavenger ecology together into the same discussion forum. Most importantly it has illustrated that scavengers can inform us about our own anthropogenic impacts on the oceans, and that baited cameras are an effective survey tool which are able to distinguish scavenging community assemblages on several scales. In addition, it has emphasised several research areas which require future attention. Models currently used in deep-sea research require improvement to increase accuracy and allow multi-species applicability, while models for abundance estimation in shallow marine environments need to be formulated. The key to enabling accurate abundance-estimation techniques and improving our general understanding of scavenger ecology in the marine environment is a fuller comprehension of odour-plume dynamics and scavenger response to odour. Hopefully these research areas will progress as technology advances and current research agendas move forward to address common research requirements within the field of scavenger ecology.

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LITERATURE CITED


Cameras and carcasses: historical and current methods for using artificial food falls to study deep-water animals

David M. Bailey¹,²,*, Nicola J. King¹, Imants G. Priede¹

¹Oceanlab, University of Aberdeen, Newburgh, Aberdeenshire AB41 6AA, UK
²Present address: University of Glasgow, Graham Kerr Building, Glasgow G12 8QO, UK

ABSTRACT: Deep-ocean animals remain poorly understood compared to their shallow-water relatives, mainly because of the great cost and difficulty involved in obtaining reliable ecological data. This is a serious issue, as exploitation of deep-water resources progresses without sufficient data being available to assess its risks and impacts. First described almost 40 yr ago, the use of baited cameras was pioneered by deep-sea biologists and is now a widely used technique for assessing patterns of animal behavior, abundance, and biodiversity. The technique provides a non-destructive and cost-effective means of collecting data, where other techniques such as trawling are difficult or impractical. This review describes the evolution of baited camera techniques in deep-sea research from the early deployments, through recent programs to investigate trends in animal distribution with depth, latitude, and ocean basin. The techniques used for imaging, baiting, and analysis are synthesized, with special consideration of the modeling techniques used in assessing animal abundance and biomass.

KEY WORDS: Deep water · Scavengers · Marine technology · Underwater cameras · Literature review · Fisheries · Stock assessment · Environmental assessment

INTRODUCTION

Baited camera deployment is a deceptively simple technique for the study of the marine environment. Simple, because at its most basic level it requires only a time-lapse camera and bait held in its field of view, but deceptive because the view of the marine environment is small and the events seen are artificial. The great advantage of baited systems is that deployment at a single site aggregates animals from a large distance around it, allowing the animals to be identified, counted, and measured. Diverse and fascinating deep-ocean scavenger communities have been revealed by such cameras, and technical and scientific advances continue to improve their usefulness. The technical improvements that allow more effective deep-water research have progressed alongside similar developments in the oil, gas, and fishing industries, bringing the threat of overfishing and habitat destruction to deep-water communities. With these dangers and the discovery of fragile habitats such as cold water coral reefs, effective deep-ocean survey and monitoring tools will become increasingly necessary.

The authors have used baited cameras for much of their work, collecting ecological, behavioral, and physiological data, and much of the material presented in the present study is from these projects and those of our immediate collaborators. It is the aim of this review to highlight the key historical advances in baited camera research and describe some of the discoveries made in baited camera surveys worldwide. This review will also illustrate the general advantages and disadvantages of baited cameras and then focus on different approaches to imaging, baiting, and data interpretation.
Baited cameras have now been deployed worldwide, to the greatest depths of the world's oceans, but with a bias towards the United States and European ocean margins. From the first baited camera experiments, the majority of studies have been undertaken with systems mounted on free-falling autonomous vehicles (also known as landers or pop-up vehicles). These vehicles consist of a frame, on which the camera system is mounted, and a buoyancy unit. The system is ballasted, usually with steel scrap, to make it negatively buoyant. The lander is then deployed by dropping it from the crane or A-frame of a ship; it sinks to the seafloor and takes photographs or video at pre-set intervals. At the end of the experiment, the ballast is dropped by the lander, usually on receipt of an acoustic command from the surface, and the lander is brought to the surface by the buoyancy unit.

Camera and water current meter data are then retrieved from the lander, batteries are recharged or replaced, and the lander is prepared with new ballast and bait for the next deployment. The use and advantages of autonomous vehicles have been reviewed by Priede & Bagley (2000) and Bagley et al. (2004). These authors particularly highlighted the great time and cost savings associated with the use of landers, allowing the deploying vessel to do other work while the lander is in the water (Table 1). In some applications, lander systems can be left in situ for months or even years. More recently, a number of other studies have been conducted by sinking carcasses and periodically visiting them with remotely operated vehicles (ROVs) or submersibles (Smith 1985), by manually placing camera systems and bait on the seafloor using these vehicles (Widder et al. 2005), or by baiting the ROV itself (Tamburri et al. 2000, Trenkel et al. 2004). The variety of vehicles used to deploy cameras, and the range of buoyancy, ballast, and release mechanisms is great and worthy of a review in itself (e.g. Jamieson 2004). This paper, however, concentrates on scientific payloads, analyses, and the results achieved. A selection of key lander systems and experiments are highlighted in Table 2.

**First steps: Isaacs and the 'monster camera'.** The first photographic lander was developed by Ewing and co-workers in the 1940s (described in Ewing et al. 1967), and was used primarily for the study of seabed features such as sand ripples. The first deep-sea baited camera was developed by Isaacs (1969) at Scripps Institution of Oceanography (University of California, San Diego). Known as the 'monster camera' (Fig. 1), this 7000 m rated lander system was deployed in the North Pacific at depths of up to 5835 m (Heezen & Hollister 1971, Dayton & Hessler 1972). Later surveys in the Pacific, Indian, and Southern Oceans demonstrated the widespread presence of an abundant and active scavenging fauna, with fish arriving at the bait

<table>
<thead>
<tr>
<th>Survey gear</th>
<th>Advantages</th>
<th>Disadvantages</th>
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<tr>
<td>Baited camera</td>
<td>Small sea time requirement for long observation</td>
<td>Lack of standardization</td>
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<td>Deployment and recovery possible from smaller vessels, with non-specialist crews and equipment</td>
<td>Many assumptions in abundance estimates</td>
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<td></td>
<td>Provides behavioral data on scavengers</td>
<td>Some taxa/size ranges do not come to bait</td>
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<td></td>
<td>Relatively non-destructive</td>
<td>Animals may be difficult to identify to species from images</td>
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<td>Bottom trawling</td>
<td>Obtains voucher specimens</td>
<td>Expensive to build equipment</td>
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<td>Abundance and biomass estimates relatively simple</td>
<td>Relatively high chance of equipment loss</td>
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<td>Historical datasets available for comparison</td>
<td>Weights of animals cannot be determined directly, and require length/weight relationships from captured specimens</td>
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<td>ROV/ submersible survey</td>
<td>Some ability to obtain voucher specimens</td>
<td>Destructive</td>
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<td>High-quality video and stills from cameras available</td>
<td>Time on bottom difficult to determine at depth, making abundance estimates less precise</td>
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<td>On rougher ground some nets fish poorly or will be damaged</td>
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<td>Ship cannot do other work while fishing</td>
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<td>Net avoidance varies between net types and taxa</td>
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<td>Few ships and individuals have the ability to trawl to abyssal depths</td>
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<td>Camera sled survey</td>
<td>Highly standardized results</td>
<td>Ship cannot do other work while dive underway</td>
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<td>Easy to tell whether camera was on the bottom</td>
<td>Camera avoidance varies between taxa</td>
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<td>Relatively non-destructive</td>
<td>Field of view and angle of line of sight vary between and during surveys</td>
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<td>Ship cannot do other work while tow underway</td>
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<td>Camera avoidance varies between taxa which are not on the bottom, unless stereo cameras are used</td>
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in <30 min in most deployments (Isaacs & Schwartzlose 1975). Amongst the animals observed off Baja California were a sleeper shark at 2039 m (Heezen & Hollister 1971) and sablefish, grenadiers, and hagfish at 1400 m (Isaacs 1969). Isaacs (1969) suggested that some apparently Arctic species, such as sleeper sharks and sablefish, were really deep-water animals that merely ‘outcrop’ at high latitudes, where cold water is close to the surface. Having shown evidence that deep-sea scavengers were abundant, Isaacs & Schwartzlose (1975) speculated that deep-ocean scavengers use odor plumes to find bait, and noted that differences in overlying productivity affected both the numbers of animals attracted and their apparent level of hunger and interest in the bait.

The observation of large numbers of active scavengers contributed to the ongoing controversy over the role of habitat complexity in supporting the observed diversity of deep-ocean species (Dayton & Hessler 1972, Grassle & Sanders 1973). Controversy on this matter raged for years, with various authors presenting contrary findings about the abundance and significance of carrion items as part of a habitat mosaic, and
disagreeing over the significance of scavengers in deep-ocean habitats (reviewed in Stockton & DeLaca 1982). Baited cameras are one of the few ways to study deep-water scavengers, as natural food falls in the deep ocean are seldom seen (Stockton & DeLaca 1982). Wilson & Smith (1984) made several important contributions to understanding the role of scavengers by using the free vehicle video (FVV) system to study the behavior of foraging abyssal grenadiers. Later, a modified version of this lander was used to make detailed measurements of the swimming speeds of scavenging amphipods (Wilson & Smith 1984, Laver et al. 1985). These studies provided key insights into the foraging methods of deep-ocean scavengers and led to first detailed descriptions of proposed energetic strategies. These, and following, studies quickly showed that deep-water scavengers possessed particular energetic characteristics, primarily, low routine metabolic rates (Seibel & Drazen 2007). Our understanding of deep-water animal energetics remains poor, and is a significant limitation to modeling their foraging behavior. As well as collecting these biological data, Wilson & Smith (1984) also made the first explicit link between the arrival rates of animals at cameras and the numbers of those same species caught by trawls in similar locations.

The search for spatial and temporal patterns. Researchers in the UK began 2 major series of baited camera experiments, which continue to widen the spatial range covered. The main areas of investigation have been to determine how depth and overlying productivity affect community composition, and how scavenger communities differ between ocean basins. The landers used were a baited version of the Institute for Oceanographic Sciences Bathysnap system (Lampitt & Burnham 1983) and the acoustic tracking experiment (ATEX) (Priede & Smith 1986). Bathysnap is a ‘free-fall camera and current meter system’ and differed from many of the systems that preceded it by resting directly on the seafloor, with the camera facing downwards at a downward angle. Usually deployed as an unbaited time-lapse photography system, the history of Bathysnap has been reviewed by Bett (2003). The initial baited (or Bathysnack) experiment, at 4009 m in the Northeast Atlantic, used the flesh of abyssal grenadiers Coryphaenoides armatus caught at the same depth. The bait was wrapped in fine cotton gauze, and attracted amphipods and fishes (but not large grenadiers) (Lampitt et al. 1983). A key finding was that changes in current direction and velocity had powerful effects on the numbers of animals seen at the bait, as Wilson & Smith (1984) observed using the FVV in the Pacific.

The first ATEX lander consisted of the FVV fitted with an acoustic tracking module and was deployed in the North Pacific in 1985 (Priede & Smith 1986). ATEX and the subsequent Aberdeen University deep-ocean submersible (AUDOS) and robust biodiversity (ROBIO) landers (Fig. 2) have since been deployed worldwide to depths of up to 5900 m. Members of this family of vehicles consist of a time-lapse stills or video camera facing downwards from a frame moored 2 m above the seafloor, kept in tension by the lander’s buoyancy (Fig. 2). The majority of ATEX and AUDOS models included an acoustic system capable of tracking ingestible transponders. These transponders were
hidden in bait packages and, once eaten, allowed the subsequent movements of the fish to be recorded at pre-selected time intervals (usually each minute) to a range of 500 m (Bagley et al. 1994). Unlike previous landers, the ATEX was baited with a single fish carcass, which was open to the scavengers. As the bait was consumed, the scavengers dispersed, allowing the processes involved in optimal foraging to be studied in the deep ocean for the first time. Arrival rates, staying times, and swimming speeds were determined for a range of scavenging fishes, allowing greatly improved estimates of scavenger abundance to be made. A key finding was that abyssal grenadiers appeared to move slowly, but continuously, with a bias towards cross-current movement, and often left the bait while some of it remained unconsumed (Priede et al. 1991). This finding linked to Charnov’s (1976) theories on optimal foraging, which showed that animals should leave a food patch once feeding opportunity at the patch dropped below the average level for the environment as a whole. A key question was whether differences in abyssal scavenger staying time could be linked to differences in the surface productivity of the overlying waters.

**Latitude and surface productivity.** The great majority of primary productivity in the ocean occurs close to the surface, which, in turn, provides food to the underlying deep-water habitats. Spatial variation in surface productivity directly influences the amount of food reaching the seafloor as particulate organic matter (C. R. Smith et al. 1997), and potentially affects the amount of carrion produced by the shallow-water nektom populations. When deployed along a transect in the North Atlantic, Bathysnap revealed a fish-dominated system on the Porcupine Abyssal Plain (southwest of Ireland), with apparent fish abundance and size decreasing to the Madeira Abyssal Plain in the south (Merrett 1987). These findings and trawl data led to the theory of a zoogeographic divide at 40° N. This theory stated that there was a lower biomass, consisting of small fish species, in the sub-tropics, where productivity was lower and more continuous, compared to in the more productive and seasonal temperate zone (Merrett 1987). When AUDOS was deployed in the abyssal Northeast Atlantic, it recorded a wide range of scavenging species, including the grenadier *Coryphaenoides armatus*, the eel *Histiotranchus bathybius*, and the ophidiids *Spectrunculus grandis* and *Barathrites* sp. (Armstrong et al. 1992). Using the AUDOS tracking data, abundance estimates were made for the Porcupine Abyssal Plain (PAP; 167 grenadiers km⁻² and 180 synaphobranchid eels km⁻²) and for the Madeira Abyssal Plain (MAP; 8 grenadiers km⁻² and 7 synaphobranchid eels km⁻²). As predicted by optimal foraging theory, staying times were longer at the oligotrophic MAP. These findings supported the zoogeographic divide hypothesis, but baited camera deployments and tagging studies further south (Cape Verde Abyssal Plain, 17° N) found elevated populations of grenadiers (Henriques et al. 2002). These studies showed that the lower abundances of *C. armatus* off Madeira corresponded with lower surface productivity, but that the seasonal upwelling system above the Cape Verde Abyssal Plain was capable of supporting large grenadiers. The surface productivity of an ecosystem could therefore be linked to the characteristics of its deep-water scavenging fauna.

**Depth.** It has long been known that community composition changes with depth, with species being found in specific depth zones (Grassle et al. 1975). Baited camera experiments confirmed trawl data showing distinct zonation in deep-sea fishes (Fig. 3). In the temperate Northeast Atlantic, baited camera data were dominated by observations of the eel *Synaphobranchus kaupii* on the upper slope (to around 1200 m), which were then replaced by morid cods *Antimora rostrata*, to about 2000 m, when they were replaced by the abyssal grenadier *Coryphaenoides armatus* (Armstrong et al. 1992, Priede & Merrett 1996, Collins et al. 1999a). Collins et al. (2005) combined trawl and baited camera data to investigate patterns in the deep-sea fish community with depth. These analyses showed that, while both biomass and abundance of fishes fell with increasing depth, patterns in body size differed greatly between scavenging and non-scavenging fishes, with the scavengers (those species seen at baited cameras) increasing in average mass with depth. This was explained by a mathematical model of fish foraging, which showed that the optimum body size for fishes depended on the characteristics of the meals they utilized. Scavengers used larger but less frequent food items, and larger size provided scavengers with the endurance necessary to travel between sporadic feeding opportunities. Differences in energetic strategy between sharks and bony fishes may also explain differences in the depth distributions of osteichthyan (bony) and chondrichthyan fishes (sharks, rays, and chimaeras). To investigate this phenomenon Priede et al. (2006) collated data for 166 baited camera deployments in the Pacific, Atlantic, and Southern Oceans, and in the Mediterranean and Arabian Seas. These data showed that the entire class Chondrichthyes is confined to waters <3000 m deep. All species in this class are vulnerable to the over fishing that is decimating shark populations (Myers & Worm 2005).

At the extreme end of the depth range, baited cameras have been used in the ocean trenches, to depths in excess of 10 km. The deepest recordings of fish were of grenadiers *Coryphaenoides yaquinae* at 5900 m.

(Priede et al. 1990) and brotulids at 5861 m (Hessler et al. 1978) in the North and South Pacific, respectively. Deeper deployments observe only scavenging crustaceans, but often in great numbers (Birstein & Vino-gradov 1955, Beliaev 1989). The true depth limits of fish distribution are not yet clear, and the mechanisms controlling the distributions of fishes are not known, as a wide range of physical (light, pressure, temperature) and ecological variables (food availability, numbers of predators) co-vary with depth. Various ecological and physiological hypotheses have been erected, but none completely explains the data (Priede et al. 2006).

**Comparing abyssal basins.** The majority of abyssal (>2000 m) baited camera experiments have been undertaken in the North Pacific and North Atlantic Oceans. In both of these oceans the abyssal plain fish community is dominated by large grenadiers. In the temperate Atlantic, the plains species is *Coryphaenoides armatus*, while in the Pacific this species is confined to the lower reaches of the ocean margins and the plains are dominated by *C. yaquinae* (Wilson & Waples 1983). The Atlantic temperate fauna is well characterized and found consistently across a wide area, but the northern and eastern extensions of this ocean are quite different. Jones et al. (2003) described the scavenging fauna of the Mediterranean Sea, demonstrating that the large grenadiers and amphipods that dominate scavenging fauna of the oceanic abyss are absent at similar depths in this enclosed sea. The abyssal scavenging fauna is numerically dominated by a shrimp, *Acanthephyra eximia* (Jones et al. 2003), which can be found around hydrothermal vents in the Atlantic (Desbruyères et al. 2001). The much greater water temperatures at depth, shorter time that the Mediterranean abyss has been habitable, and the shallow sill (<300 m deep), which separates this sea from the Atlantic, are all possibly responsible for preventing the entry of the ‘normal’ oceanic fauna. To the north, above the Arctic Circle, grenadiers are also absent, and the abyssal scavenging fauna is dominated by amphipods (Klages et al. 2001); higher up the slope the main scavenging fish are zoarcids (Premke et al. 2003). Lower temperatures in the Arctic might be a factor, but it is interesting to note that in the abyssal Arabian Sea zoarcids are also among the dominant scavenging fish species seen by baited cameras and large grenadiers are very rare (Janßen et al. 2000). Like in the Atlantic, in the southern Indian Ocean the abyssal fish community appears to be dominated by large *C. armatus* (King 2006).

**Temporal patterns.** Spatial patterns have been extensively examined, but temporal patterns are extremely poorly characterized. Seasonal comparisons using acoustic tracking (Priede et al. 1994b) and video analysis (Priede et al. 2003) showed changing levels of
swimming activity in abyssal fishes, but these could also have been caused by interannual changes in nutritional state (Drazen 2002). Changes in length-frequency distribution indicated that migrations by grenadiers may have occurred (A. Smith et al. 1997, Priede et al. 2003), but confirming this will require much more data.

TECHNOLOGY FOR SURVEY AND SCIENTIFIC STUDIES

While deployment methods differ, all systems require a camera, light, and a means of attracting animals. The choice of each item depends on the specific aims of the deployments (e.g. from survey to behavioral study) and how well characterized the fauna is prior to deployment.

**Camera systems.** There are many options to be considered, including the sizes and angles of the fields of view, the type of lighting, and between video and still photography. The Bathysnap and ‘Eye In The Sea’ (Widder et al. 2005) vehicles used oblique photography, providing a larger field of view, and good side views of the animals, making them potentially easier to identify than in top-down images. One disadvantage of this technique is that from a single camera it is impossible to estimate the sizes of animals which are not touching the seafloor (animals on the bottom can be sized using a ‘Canadian grid’ superimposed on the image). Oblique angled photography is mainly used for unbaited deep-sea photography, where most of the animals of interest are on the seafloor (Kauffman & Smith 1997, Bett et al. 2001). One other potential disadvantage of baiting an obliquely angled camera is that the results obtained may be affected if the camera’s supporting structure is touching the seafloor. Jamieson et al. (2006) recently described how fish often ignore the bait and investigate lander frames, potentially making them invisible to the camera for long periods of time. For this reason, Jamieson et al. (2006) recommended that lander or mooring parts coming close to the seabed should be within the field of view of the camera.

The ‘monster camera’ used a downward-facing camera, tethered off the seafloor to maximize the field of view. This system was adopted in the design of the FVV (and its descendants ATEX, AUDOS, and ROBIO), using a measured scale-bar close to the seafloor. By using this reference length and calculating the range of bentho-pelagic animals from the position of their shadows on the seafloor, the lengths of animals can be calculated from a single camera, even when they are not in contact with the seafloor. However, the accuracy of the estimates falls dramatically as the animals get further from the seabed and the reference scale (N. King & D. Watson unpubl. data). With a downward-facing camera there is clearly a trade-off between the seafloor area visible and the amount of detail available in the images, usually determined by the camera’s range from the seafloor. Placing the camera closer and using a wide-angle lens is an attractive option, but causes measurement artifacts if lengths and swimming speeds are to be determined from images or video sequences.

Most baited camera deployments undertaken for survey and census reasons have used stills cameras, mainly because the increased resolution available from film made species identification easier. However, recordings of swimming movement from video can also be used when classifying organisms. Video has been used by several teams to collect information on locomotory performance and behavior in deep-sea animals. One recent example is the ‘Sprint’ lander, which used video in conjunction with an electrical stimulator to elicit burst swimming performances from fish and shrimps attracted to bait, allowing their muscle power output to be estimated (Bailey et al. 2003). Collins et al. (1999a) used video data, alongside acoustic tracking, to show how fish activity levels are reduced at greater depths, probably as a consequence of lower food availability.

Current high-resolution, color video cameras require relatively large amounts of light. For example, the Sprint lander used twin 75 W incandescent lamps (Bailey et al. 2003). Long periods of illumination at such light intensities sometimes affect the behavior of the animals that the camera is there to observe. The bathyal eel *Synaphobranchus kaupii* slowly moved away from the camera field of view when lit (Bailey et al. 2005), but the abyssal grenadier *Coryphaenoides armatus* did not avoid the lights used to illuminate it (Wilson & Smith 1984). Recent studies suggest that *S. kaupii* interacts with bioluminescent ostracods during scavenging (Heger et al. 2007), and reacting to their light may be a natural behavior for these fishes. Other bathyal fishes, such as toothfish, also react to the lights of video landers (Collins et al. 1999b), and, like the eels, this may be because light has some ecological relevance to this species, perhaps during a shallower-living point in their life cycle.

One solution to the lighting problem is to use a high-frequency acoustic camera, to which the fishes should be completely oblivious, but under most conditions the image quality and field of view are not as good as those of optical cameras (Rose et al. 2005). More conventional active sonars provide much greater fields of view (K. L. Smith et al. 1989), but are currently best used in conjunction with cameras (Premke et al. 2003). Camera systems using red-light illumination appear to dis-
turb fish less than those using white light, resulting in greater numbers of scavenging animals, while providing sufficient light for video recording (Widder et al. 2005).

**Baits and other attractants.** After setting up all the high-tech hardware, the camera must be baited. This is a critically important part of the procedure, as small details in the size, type, and configuration of the bait affect the results obtained. The most common baits are shallow-water fishes, either in a leaky container or open to the scavengers. In either case, scavenging animals are attracted by the production of an odor plume that stretches downstream of the baited camera. This is a very cheap and effective means of attracting animals to the camera from a large area, but suffers from some significant disadvantages. The baits used are not standardized between research groups, making comparison of results difficult, as the rate of odor release and the length of time that the bait lasts depend completely on the type of fish used (Lampitt et al. 1983) and how it is prepared (homogenate, fillets, whole). The early experiments tended towards enclosed baits, but, following Priede & Smith (1986), many teams now use open baits to mimic small natural food falls. With such open baits there is a feedback process between the numbers and sizes of the scavengers attracted and the length of time that the bait remains attractive (Collins et al. 2002). This probably makes the results obtained less consistent between deployments, and details of how the bait is attached to the camera system greatly affect how long it remains visible. Bait mixes enclosed in a mesh container or released by a pump are probably more consistent between deployments than whole fish, but the form and duration of the feeding frenzy produced cannot mimic events at a natural carrion fall. Monterey Bay Aquarium Research Institute researchers used liquidized fish, emitted by a pump, to attract mobile animals in an experiment to test the effects of deep-ocean carbon sequestration on deep-living animals (Tamburri et al. 2000). This bait was so effective that the fish remained present even when the pH of the water around the bait source was reduced from 7.6 to 5.6 by CO₂ hydrate pumped from the ROV. While most researchers use fish in some form as bait, plant remains have also been used. Traps baited only with sea grass and seaweed captured amphipods at depths of 10 and 500 m off the Bahamas (Lawson et al. 1993).

Changing the type and configuration of the bait affects both the numbers of animals seen and the species observed. The Bathysnap system observed *Pachycara bulbiceps*, which was not observed at the same locations by Armstrong et al. (1992), but did not observe *Coryphaenoides armatus*, the dominant fish scavenger at that depth. Bathysnap has always used enclosed baits and tends to be deployed for longer durations than the AUDOS lander with its open bait (usually a single Atlantic mackerel *Scomber scombrus*). The greater persistence of the protected bait allows zoarcids to arrive and exhibit the ‘roosting’ behavior for which they are now well known (Witte 1999, Janßen et al. 2000, Kemp et al. 2006).

One disadvantage of small, unprotected baits is that the experiment is over very quickly (often within hours of lander touchdown), but Kemp at al. (2007) deployed a recently developed periodic bait-release system during a long-term lander experiment on the Mid-Atlantic Ridge. The periodic bait-release contained several individual fish carcasses in sealed tubes, which were released singly at pre-determined intervals. The system produced replicate baited experiments, with grenadier fishes apparently leaving the lander after feeding and being attracted when new bait was released. The sealing of the bait within the tubes and the deactivation of surface-dwelling microorganisms by the environmental pressure appeared sufficient to retain the freshness of the bait between bait releases. This system has great potential for the study of scavenging animals during periods when ship operations are impractical, such as during winter at higher latitudes.

The largest baits used on landers are the carcasses of small marine mammals (Jones 1999, Kemp et al. 2006), which attract very large numbers of scavenging fishes and invertebrates for periods of several weeks. Such studies have provided fascinating information on deep-water ecology and, in particular, on the interactions between species. For example, Kemp et al. (2006) showed that changes in numbers of crabs feeding on the carcass of a porpoise fluctuated violently, but the drops in crab numbers were associated with the presence of predatory octopods. There have been several studies of large marine mammal carcasses, made by sinking them into deep water with large weights and then visiting them periodically with ROVs and submersibles (Smith & Baco 2003). The succession of animals at whale carcasses, began with a ‘mobile scavenger’ phase, similar to that seen at baited landers, ending with a ‘reef’ stage, when the nutritional content of the skeleton has been exhausted by sulphophilic organisms and the bones have been colonized by suspension feeders (Smith & Baco 2003). The observation of chemoautotrophs feeding at whale carcasses led to the ‘stepping stone’ theory, which suggested that whale carcasses might provide the necessary habitat to support the dispersal of vent animals from one hydrothermal fluid source to the next (C. R. Smith et al. 1989).

The above techniques attract animals by an odor plume and perhaps also by an acoustic/mechano-receptor signal from the impact of the carcass on the...
Comparisons of the species lists generated by baited camera and trawl censuses often differ greatly, as baited cameras usually only attract scavengers. In the NE Atlantic only 18 species were attracted to bait compared with 71 species taken within trawls (Priede et al. 1994a, Priede & Merrett 1996). A recent survey of demersal fish species on the Mid-Atlantic Ridge also detected 22 species at baited landers, 40 species on a series of 1000s of baited long-line hooks, and 80 species in Campelen trawls (King et al. 2006, I. Fossen et al. unpubl. data). In a recent global comparison, more than twice as many species were found at any depth with otter trawls (OTSBs) than with baited cameras (Priede et al. 2006).

Calculating animal abundance and biomass. A more significant challenge than determining that a species is present is to estimate the true abundances of that species in the wider environment. The number of animals at the bait changes continuously during the deployment (Fig. 4), often resulting in a feeding frenzy of fish and crustaceans filling the camera field of view (Fig. 3). Interpreting these data requires information or assumptions about the sensory abilities and foraging method of the animals and about the behavior and area of influence of the odor plume after it has left the camera system.

The scenario used in the present generation of models is that the odor is carried downstream by the current and either reaches a stationary animal, or that animal swims into the odor plume while actively searching for food (Priede & Merrett 1996, Bailey & Priede 2002). The length and spread of the odor plume (and thus the number of animals which it contacts) are determined by the current velocity (and so a current meter is usually fitted to the lander). Upon contacting the odor, rheotaxis is triggered, and animals use the odor plume gradient to stay within the plume until they reach the baited area. They then locate the bait, feed until the bait is consumed, or leave sooner if they estimate that better feeding opportunities exist elsewhere (Charnov 1976). There are major differences between species in their tendency to remain in the vicinity of baits, and it is very difficult to determine individual staying times unless acoustic tagging is used, or a fish has an unusual distinguishing feature such as a prominent ectoparasite. The number of animals at any one time, therefore, depends on the current velocity, movement speeds of the animals (which may also be affected by current velocity), and how long the animal stays at the bait (which is determined by both its feeding rate, the actions of other animals, the bait characteristics, and the number of other feeding opportunities).

The earliest abundance calculation model was a ‘sit and wait’ model for crabs, developed by Sainte-Marie
& Hargrave (1987), and subsequently refined by Collins et al. (2002). This latter model used the arrival rate and estimates of effective plume area to estimate abundance from the arrivals of many animals and is therefore a very robust measure. These models assume Gaussian odor plume dispersal, that every individual of the focal species responds similarly to the odor of the bait, and that all the animals attracted remain at the bait throughout the recording. Priede et al. (1990) proposed a simple model for the calculation of fish abundances based on their first arrival time and allowing for the dispersal of fish after feeding (Fig. 4C). The model was easy to implement and produced abundance estimates which were close to those of otter trawls done at the same locations (Fig. 5A) (Priede & Merrett 1996). This model is the basis of all the abundance estimates for AUDOS and ROBIO deployments described in this review. In an effort to develop models that described the data more accurately, Bailey & Priede (2002) developed models that allowed for ‘sit and wait’, ‘cross current foraging’, and ‘drifting’ behavior patterns. Although the newer models appeared qualitatively to mimic ‘real’ deployment data more closely, the greatly increased difficulty of using them for abundance estimates cannot be justified on the basis of the available field data. Results from this model are shown in Fig. 5B, comparing abundance estimates from a towed camera sled to those from the Sprint video lander. Farnsworth et al. (2007, this Theme Section) criticised the use of deterministic models for abundance estimates, and presented a model which used more of the data available from arrival time patterns. Careful field trials and a statistical analysis of the model predictions will be required to determine which models are the most appropriate for the analysis of baited camera data.

Once abundances have been estimated, scavenger biomass can be calculated, using animal dimensions and allometric relationships. In comparison with trawl data in the NE Atlantic, landers sampled a more limited size range, not fully representing juveniles and very large specimens of Coryphaenoides armatus. Noting this difference in size frequency led to the discovery that brain morphology changes throughout life in C. armatus as its niche changes ontogenetically (Wagner 2003).

Data gaps. There are significant gaps in our understanding of both odor plume and animal foraging behavior. For instance, we know little about the odor sensitivity of deep-sea animals, or how the odor plume disperses, especially in rough terrain such as reefs and canyons (Fig. 5C). While the AUDOS tracking system has provided much useful behavioral information, these data could only be collected after the animal had fed (and eaten the transponder) and therefore could not describe the animals’ previous actions (e.g. its reaction to the plume). At this time we lack critical information on energetic strategies, such as which animals remain stationary on the seafloor until contacted by an odor plume (Wilson & Smith’s [1984] ‘sit and

Fig. 4. (A,B) Numbers of fish within view of the camera over time after touchdown at 911 m, Nazaré Canyon, Portuguese coast. Each vertical histogram bar represents 1 image frame with fish visible. (A) Data for Synaphobranchus spp. and (B) the other taxa recorded. Bars: the most common taxa attending bait; black bars: Mora moro; dashed bars: Trachyrincus scabrus (?). Symbols: less common visitation; crosses: Hexanchus griseus (?); open circles: Deania sp.; open triangles: unidentified sharks; filled diamonds: Phycis sp. (? = species identification uncertain). The bait was not completely consumed during the deployment. (C) Numbers of Coryphaenoides armatus as a function of time (maximum number per 10 min interval) at 3400 m, Nazaré Canyon. Raw deployment data are represented by open circles and closed squares for each of 2 deployments. Grey line: mean number of individuals for the 2 deployments; black line: smoothed ‘shark’s fin’ model fitted values (Priede et al. 1990)
wait’ strategy) and which animals search across currents as other authors have suggested (Barnes 1955, Priede et al. 1991). Basic sensitivity analyses have shown how abundance estimates are greatly affected by assumptions concerning an animal’s foraging method (Bailey & Priede 2002) and swimming speed (Yau et al. 2000), so some of these data gaps will need to be filled if we are to have confidence in lander abundance estimates.

**SUMMARY**

Baited cameras gave us our first view of a diverse, abundant, and active scavenging fauna in the dark ocean abyss, and, in many cases, deploying baited cameras is still one of the most effective ways of obtaining biological information from deep water. Worldwide surveys have shown patterns in scavenger behavior, abundance, and diversity with latitude, depth, and between oceans. Despite long experience in the use of these camera systems, many data gaps remain, which make interpreting the images obtained more difficult. The choice of camera system and bait and the amount of background information available about the environment and the focal species make a great deal of difference to the success of the data interpretation. All survey techniques have assumptions. The avoidance and attraction effects of moving survey gears such as trawls, camera sleds, and ROVs are poorly known for deep-sea animals, affecting their effective search area in much the same way that errors are caused in baited camera surveys (Trenkel et al. 2004). Baited cameras have a long history, and, with care, their deployment provides an efficient means of studying the distribution, behavior, and abundance of deep-sea animals.

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Response of deep-sea scavengers to ocean acidification and the odor from a dead grenadier

James P. Barry1,*, Jeffrey C. Drazen2

1Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California 95039, USA
2University of Hawaii, Department of Oceanography, MSB 606, 1000 Pope Rd, Honolulu, Hawaii 96822, USA

ABSTRACT: Experiments to assess the impact of ocean acidification on abyssal animals were performed off Central California. The survival of caged megafauna (Benthoctopus sp., Pachycara bulbiceps, Coryphaenoides armatus) exposed to CO2-rich and normal (control) seawater varied among species. Benthoctopus sp. and P. bulbiceps survived control conditions and month-long episodic exposure to acidic, CO2-rich waters (pH reductions of ~0.1 U). All C. armatus in both treatments died, potentially due to cage-related stress, predation, and exposure to acidic waters. High survival by P. bulbiceps and Benthoctopus under month-long exposure to CO2-rich waters indicates a physiological capacity to cope, at least temporarily, with stresses that will accompany expected future changes in ocean chemistry. The abundance of free-ranging scavengers was not correlated with variation in pH levels near fish cages. Incidental observations of abyssal scavengers collected using time-lapse cameras during these experiments were used secondarily to evaluate the hypothesis that macrourid fishes avoid the odor of dead conspecifics. Caged macrourids in view of time-lapse cameras died within 2 to 3 d, eliciting a strong response from the regional scavenger assemblage which aggregated near the cage. The pattern of scavenger visits suggests avoidance among taxa and a succession of scavengers. Macrourids, a dominant abyssal scavenger, either did not respond to the death of their congener or possibly avoided the area. Lack of a response by macrourids may be due to (1) avoidance of sites of dead or dying congeners, (2) high sensitivity to ocean acidification, (3) low nutritional value or weaker odor plumes from carcasses of abyssal versus shallow-water taxa, or (4) rapid departure from sites where a carcass is inaccessible. Camera systems were not deployed in view of carcasses at control sites (away from CO2 pools) during each experiment, and we therefore cannot exclude the possibility that the pattern of scavenger visits was influenced by elevated carbon dioxide levels.

KEY WORDS: Food fall · Behavior · Macrouridae · Coryphaenoides armatus · Zoarcidae · Pachycara bulbiceps · Octopodidae · Benthoctopus sp.

INTRODUCTION

The rise in ocean CO2 levels due to the passive flux of carbon dioxide through the air–sea boundary is causing rapid and dramatic change in the carbonate chemistry of the oceans. Higher carbon dioxide levels react with the carbonate chemistry of seawater to increase ocean acidity. Rising ocean carbon levels have caused the pH of ocean surface waters to drop by 0.1 U in only the past 50 yr (Caldeira & Wickett 2003). Anthropogenic carbon dioxide is now detectable to ocean depths of 1 to 3 km, as the surface carbon signal penetrates slowly into the deep sea (Sabine et al. 2004). Deep-ocean carbon sequestration, a concept considered to mitigate the rapid rise in atmospheric carbon levels, could also result in severe acidification of deep-sea waters, at least near disposal sites (Shirayama 1998). Projections of future ocean carbon levels indicate a reduction in surface ocean pH of 0.4 U by 2100, and may reach –1.0 U over the next few centuries (Caldeira & Wickett 2003). This signal will mix and propagate through the water column and could...
have a significant impact on ocean ecosystems (Orr et al. 2005, Raven et al. 2005). CO₂-related stresses for ocean organisms exposed to CO₂-rich, acidic waters include reduced calcification, respiratory stress, disruption of the acid–base balance, and metabolic depression (Pörtner et al. 2004a). The severity of CO₂-related stress is expected to be considerably greater for deep-sea organisms (Seibel & Walsh 2001), but little research has addressed this issue directly.

In the current paper we present results from a series of field experiments off Central California to evaluate the tolerance of abyssal animals to elevated CO₂ levels. We focus on a few species of common abyssal scavengers (the octopus Benthoctopus sp. [Octopodidae], the eelpout Pachycara bulbiceps sp. [Zoarcidae], and the grenadier Coryphaenoides armatus [Macrouridae]), which were captured in baited cages, then held in CO₂-rich, acidic waters and in control locations during month-long experiments. Although the sensitivity of the 2 abyssal fishes to ocean acidification is not known, some information is available concerning the behavioral and physiological responses of deep-sea megafauna to elevated carbon dioxide levels. Seibel & Walsh (2003) showed that moderate (~0.3 pH U) acidosis of the blood of Benthoctopus sp. reduced oxygen binding by hemocyanin by 40%. Pachycara brachycephalum, a bathydemersal congener of P. bulbiceps, undergoes a ~35% reduction in oxygen consumption in cell suspensions with a 0.6 U pH reduction (Langenbuch & Pörtner 2003), but little is known of the response of live animals. Tamburri et al. (2000) evaluated the response of benthic scavengers exposed to CO₂-rich waters or filtrate from homogenized shallow water fishes or both, finding that various scavengers were attracted strongly to the food odor, even with the strong narcotizing effects of the CO₂-rich plume. For smaller abyssal organisms, our previous results have shown that sediment-dwelling meiofauna experience significant mortality after month-long exposure to pH reductions of ~0.1 to 0.3 U (Barry et al. 2004, Thistle et al. 2005).

A secondary focus of the present paper, based on incidental time-lapse observations of the abyssal scavenger assemblage collected during these ocean acidification experiments, was to evaluate the behavioral response of abyssal scavengers to the odor plume from dead macrourid fishes. Following the unexpected death of Coryphaenoides armatus held in cages during ocean acidification studies, we observed the response of the scavenger assemblage to these ‘food falls’.

A variety of factors influence the scavenger assemblage observed in baited camera studies. Scavenger assemblages vary by region, with decreasing species richness with depth (Priede & Bagley 2000, King et al. 2006), and respond variably to the type, size, and position of bait (Wolff 1976, Rowe et al. 1986, Armstrong et al. 1991, Witte 1999, Bailey et al. 2002, Kemp et al. 2006). At bathyal depths, megafaunal invertebrates are important scavengers (e.g. Smith 1985, Witte 1999), while at abyssal depths lysianassid amphipods and macrourid fishes are among the first and most abundant scavengers to arrive at food falls (Isaacs & Schwartlose 1975, Priede et al. 1991, Jones et al. 1998, Priede & Bagley 2000). Bait used in time-lapse camera studies typically consists of shallow-water fishes or occasionally plants, and has ranged widely in size from single mackerel (Priede et al. 1994, Smith et al. 1997) to cetacean carcasses (Witte 1999, Smith et al. 2003, Kemp et al. 2006). Small to medium food falls are typically consumed within hours (Priede et al. 1994, Jones et al. 1998), resulting in a pattern of scavenger arrival and departure related to foraging behavior (Bailey & Priede 2002).

Although grenadiers (Macrouridae) are common abyssal scavengers, their response to the odor plume from congeners or conspecifics is known poorly, since nearly all available studies have used shallow-water plants or animals as bait (but see Lampitt et al. 1983). Unlike the odor plume from sunken carcasses of shallow-water species, the scent from a dying or dead conspecific may indicate a potentially dangerous site, and it may be adaptive for benthic scavengers such as grenadiers to ignore or avoid such odors. Although the cause of death is likely indeterminable from the odor plume, recent mortality may indicate elevated risk of mortality for conspecifics, such as the presence of predators or risk of infectious disease. Thus, a balance between risk of starvation and predation or infection may influence scavenger behavior (McKillup & McKillup 1992, 1994). Increased fitness associated with avoidance of sites with higher than average rates of injury or death may have led to selection for behavioral responses to remote cues indicative of increased risk. For example, elevated risk of mortality appears to reduce the abundance of vulnerable life-history phases (juveniles & brooding females) of the lysianassid amphipod Orchomene nanus to food falls (Moore & Wong 1995). Aversion to odor plumes from dying or recently dead conspecifics, as observed in several epibenthic scavengers (Moore & Howarth 1996), may be an evolutionarily derived adaptation to reduce exposure to potential sources of mortality. In the present paper we describe the pattern of scavenger visits in response to odor plumes from dead grenadiers, and consider the hypothesis that macrourids are averse to the odor of dead or dying conspecifics.

The goals of the experiments described in this paper focused primarily on the effects of ocean acidification on abyssal scavenger species. Unplanned observations of the response of the scavenger assemblage to the
death of grenadiers held in cages for the acidification studies formed the basis for novel observations of scavenger behavior at an abyssal food fall. This study differs from typical food fall studies in 2 significant ways. First, the time-lapse observations focus on caged macrourids that did not produce an odor plume stimulating scavengers until their death 3 to 4 d into the observations. In addition, the attractant was the odor from a decaying macrourid, rather than a shallow-water species.

**MATERIALS AND METHODS**

**Effects of ocean acidification.** A series of approximately month-long experiments (E1, E2, E3) used to evaluate the tolerance of abyssal scavengers to ocean acidification was performed at 3100 to 3600 m depth on the flat, relatively featureless seabed of the continental rise off Central California (E1 & E2: 36.712°N, 123.525°W, E3: 36.7°N, 123.006°W, Fig. 1a, Table 1). During 2 experiments (E1, E2) demersal and benthopelagic scavengers (Macrouridae, *Coryphaenoides armatus*; Zoarcidae, *Pachycara bulbiceps*; Octopodidae, *Benthoctopus* sp.) were held in cages positioned at sites with CO₂-rich, acidic waters (treatment) and control sites with normal ocean chemistry. Study animals were captured during a short period (1 to 2 d) prior to each experiment, in cages baited with mackerel or squid. At the start of each experiment, the cages were locked closed to prevent further ingress or egress. For E1, a small amount of bait remained in the cage and continued to attract scavengers, at least during the beginning of the experiment. In E2, the bait was removed prior to the start of the experiment to inhibit the attraction of additional scavengers. During E3, a time-lapse camera system was deployed to observe a CO₂ corral and nearby area, but baited cages were not deployed to capture benthopelagic scavengers. Thus, no odor plume from dead or dying caged megafauna was present during this experiment, and time-lapse observations are more representative of the background densities of animals, particularly prior to injection of liquid CO₂ into the corrals. The original purpose of these experiments was to assess the effects of hypercapnia on deep-sea benthos (Barry et al. 2005).

High CO₂ conditions were created by releasing liquid carbon dioxide (20 to 100 l) into small corrals (sections of PVC pipe) placed on the seabed using the remotely operated vehicle (ROV) ‘Tiburon’, operated by the Monterey Bay Aquarium Research Institute. Because deep-ocean waters are undersaturated with carbon dioxide, the liquid CO₂ dissolves slowly into seawater, forming a high-CO₂, low-pH dissolution plume, which mixes with the ambient current and drifts downstream over sediments and any animals nearby.

The arrangement of the CO₂ corrals varied. For E1, a single 100 l pool was created and caged animals were positioned from 0.5 to 50 m away (Fig. 1b). In E2 a circular pattern of CO₂ pools (n = 7 corrals) was used, with cages

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**Table 1. Summary of CO₂-tolerance experiments and time-lapse observations.** Start and end: dates for the initiation and termination of each experiment; TL: length in days of the time-lapse observations. The number of fish traps (cages) and distances (m) from CO₂ pools are also listed.

<table>
<thead>
<tr>
<th>Expt</th>
<th>Latitude (°N)</th>
<th>Longitude (°W)</th>
<th>Depth (m)</th>
<th>Start</th>
<th>End</th>
<th>TL (d)</th>
<th>Cages</th>
<th>Distance (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1</td>
<td>36.712</td>
<td>123.525</td>
<td>3600</td>
<td>2 Apr 2002</td>
<td>2 May 2002</td>
<td>24.8</td>
<td>8</td>
<td>1 to 50</td>
</tr>
<tr>
<td>E2</td>
<td>36.712</td>
<td>123.525</td>
<td>3600</td>
<td>19 Dec 2003</td>
<td>19 Sep 2005</td>
<td>8.9</td>
<td>8</td>
<td>1 to 75</td>
</tr>
<tr>
<td>E3</td>
<td>36.700</td>
<td>123.006</td>
<td>3100</td>
<td>13 Dec 2004</td>
<td>21 Jan 2005</td>
<td>8.6</td>
<td>0</td>
<td>–</td>
</tr>
</tbody>
</table>
placed within the circle and at a control location ~100 m away (Fig. 1c). During E3, CO2 corrals were configured similar to E2 (Fig. 1c), using 14 corrals, and no fish cages. At the end of these month-long experiments, we compared the survival of treatment (high CO2) and control (normal CO2) groups.

Physical conditions, including the strength of the dissolution plume (pH changes were used as a proxy for CO2 levels) and variation in the speed and direction of bottom currents were measured by instruments deployed near cages and CO2 pools at the experimental sites. Conductivity, depth, and pressure were measured with CTDs (SeaBird Model 19+), which were each also equipped with 2 SeaBird Model 18 pH sensors. These sensors, positioned at various distances from the animal cages and CO2 corrals during each experiment to measure variation in seawater chemistry, recorded the temperature, salinity, pressure, and pH at 5 min intervals throughout the experiment. pH sensors were positioned from 5 to 50 cm above the seabed to measure the potential spatial variation in the dissolution plume. Near-bottom currents were measured at 5 min intervals during each experiment using an acoustic doppler current meter (ADCP; RDI Sentinel, 600 mHz) mounted 2 m above the seabed, fixed in an upward-looking orientation. Measurements 7 m a.b. (meters above bottom) were the records nearest the seabed and were used to characterize the local flow pattern. Although it would be preferable to measure flow nearer the seabed (e.g. 1 m a.b.), this was not possible using the equipment available. Additional details of these experiments are available in Barry et al. (2005).

**Time-lapse camera observations.** A time-lapse imaging system was deployed during each experiment with a primary objective of observing rates of dissolution from CO2 pools and the behavior of caged animals under elevated CO2 levels. Observations of the behavior and abundance of scavengers in the vicinity of the cage before and after the death of caged macrourid fishes were incidental, but are the basis of the results presented below concerning factors influencing scavenger behavior. A single camera system was available, and it was positioned strategically to view at least part of a CO2 pool for observations of CO2 dissolution, and also in view of a cage (E1, E2) to observe animal behavior. Because scavenger observations were not an initial objective of these experiments, time-lapse observations were not made at control sites, and, thus, all time-lapse images are at CO2-treatment sites.

For E1, a monochrome, time-lapse video camera equipped with LED lights was positioned to view the CO2 pool and the nearest cage (~1 m away) containing *Coryphaenoides armatus* (n = 2) and *Pachycara bulbiceps* (n = 1) (Fig. 2a). Video (Hi-8 format) was recorded in hourly intervals (8 s interval−1) from 4 April to 1 May 2002. For E2 and E3, a Seasnap 990 camera system equipped with twin 100 mW incandescent lights was used to obtain time-lapse images. During E2, the camera system was positioned to view a CO2 corral and a full, side-view of the closest cage (Fig. 2b,c). The cage, positioned ~1 m from 1 of the CO2 corrals, contained *C. armatus* (n = 1) and *Benthoctopus* sp. (n = 1). Single digital images were captured every hour for 8.2 d from 21 to 29 August 2003, at which time the low battery power terminated the image sequence. For E3, the Seasnap system was positioned to view a CO2 corral and the nearby seabed (Fig. 2d). No caged animals were used during E3. Digital images were recorded every 2 h for 206 h from 14 to 23 December 2004.

The position and condition of the caged *Coryphaenoides armatus*, *Pachycara bulbiceps*, and *Benthoctopus* sp. were noted for each recording interval of E1 and E2. For E1, the position within the cage for *C. armatus* and *P. bulbiceps* was coded as 1 (top one-third of cage), 2 (middle one-third), and 3 (bottom one-third). For E2, the poorer quality of images restricted observations, and counts were made of the number of *C. armatus* and *P. bulbiceps* swimming in the top one-half of the cage. Spearman’s rank correlation tests comparing the position of the 2 caged species for each experiment were performed using observations during the period prior to the death of the macrourids, and after their death when scavengers were present near the carcass.

**Scavenger behavior.** In addition to quantifying the position of animals within cages, all identifiable organisms observed in each image of the time-lapse series from each experiment were identified and counted. For Seasnap images (E2 & E3) the identity of nearly all fishes and octopuses was clear, though for a few cases identification to the species level was questionable. Congeners of *Coryphaenoides armatus* and *Pachycara bulbiceps* live in the study region, but are quite rare. Therefore, we assumed that all macrourids observed were *C. armatus* and all large zoarcids were *P. bulbiceps*. This assumption is supported by collections of several individuals of each species during the studies. Due to image quality of the monochrome video system and the long exposure time (1 s) used for the Seasnap digital image system, small, rapidly moving objects were rarely identifiable, and appeared as small ‘streaks’ in images. Many of these objects could be benthepelagic scavengers such as lysianassid amphipods, but were not considered for analysis.

Observations of scavengers during each experiment were divided into several phases based on the shifting pattern of behavior or activity. The ‘Pre-cage’ period (Fig. 2b) preceding the placement of the cage in view of the camera (E2 only) was used to assess the background abundance of animals in the area. Observa-
Activity in and around the caged animals shifted markedly from a ‘Live’ period (e.g. Figs. 2d & 3a) prior to death of the caged macrourids to a ‘Scavenging’ phase (Fig. 3b,c) following their death. Large megafaunal scavengers were most active during the Scavenging phase, then dwindled in number during the ‘Consumed’ phase (Fig. 3d). During the Consumed phase, lysianassid amphipods and other small scavengers continued to consume the carcasses, but these scavengers were not clearly visible in time-lapse images.

The percentage frequency of occurrence of each organism observed was compared between periods, and Spearman’s rank correlation coefficients were calculated for some pairs of species between Live and Scavenging periods to assess potential avoidance or aggregation. Correlation analyses were used to evaluate the hypothesis that scavenger abundance declined with higher CO$_2$-related stress, as measured by pH reductions. Thus, we calculated correlation coefficients between observed pH and the abundance of common scavenger species for each experiment.

**RESULTS**

**Physical conditions**

Near-bottom currents were similar among sites and experiments. Conditions measured during E2 are presented here to represent flow at all sites. Currents 7 m above the seabed were variable in direction and in speed, but always quite sluggish. Flow varied from 0 to 8.7 cm s$^{-1}$, with an average of 3 cm s$^{-1}$ during time-lapse observations. Net flow varied among experiments, but flow direction typically oscillated greatly, and generally rotated with the semidiurnal tides (Barry et al. 2005).
The severity and persistence of CO2 treatments were similar among experiments and distance from CO2 pools, as recorded by sensors near caged animals. Dissolution of liquid CO2 pools was slow, apparently due to the sluggish bottom currents at the sites (Barry et al. 2005), producing only mild reductions in pH. During E1, pH perturbations were episodic and short-lived, ranging from 0 to -0.3 U at a distance of 5 m from the large CO2 pool (Fig. 4a). The largest pH changes were measured during the latter half of the experiment, after the CO2 corral was refilled with liquid CO2. pH sensors within 0.5 m of the large CO2 corral failed, but measurements close to CO2 corrals in other experiments have shown pH reductions >1 U.

During E2, pH changes in the center of the circle of CO2 corrals were also episodic and milder than in E1 (Fig. 4b). Variation in pH was greatest during the first 3 to 4 d of E2 (Live phase), with occasional excursions greater than -0.15 U. After this period, pH variability was low and average values were near (within ~0.05 U) ambient. The CO2 corrals were not refilled during E2, and much of the liquid carbon dioxide had dissolved by the end of the month-long experiment. The pattern of pH variability during E3 (not shown) was very similar to that during E2.

**Effects of CO2 treatments**

There was no detectable response by caged or free-ranging megafauna after a month-long exposure to the mild acidic dissolution plume emanating from pools of liquid CO2. All caged Benthoctopus sp. and Pachycara bulbiceps survived at both the CO2-treatment and control locations. In contrast, all caged Coryphaenoides armatus died, regardless of treatment. The abundances of free-ranging scavengers, either overall (total scavenger abundance) or for individual species, were not correlated to pH measured near caged fishes during E1 or E2.
Because the odor plume and CO₂-related acidification could have simultaneously affected scavenger behavior (e.g. Tamburri et al. 2000), the effects of CO₂ alone can only be assessed prior to the death of the caged fish. If the analyses of CO₂ effects are limited to the live period prior to any influence of an odor plume and when at least some significant variation in pH occurred in both experiments, there was still little evidence of a response to elevated CO₂ levels by either scavengers or non-scavenger species. No significant correlations between pH and the abundance of any of the principal species observed in E1, E2, or E3 were detected. Nor did any animals display an adverse reaction to the acidic dissolution plume.

Caged animal behavior

The behavior of caged animals exposed to elevated CO₂ levels varied among species. Coryphaenoides armatus typically swam near the top of cages, declining and dying within a few days in E1 and E2 (Fig. 5). One caged macrourid in E1 may have died after only ~30 h, based on its unchanging position on the bottom of the cage after this period (Fig. 5a). Pachycara bulbiceps rarely swam above the bottom of the cage (Fig. 5b), and was sedentary and generally motionless when visible during E1. Caged P. bulbiceps were not observed to consume C. armatus tissue during any of the 8 s video clips recorded in E1, even though it increased greatly in abundance outside the cage upon the macrourid’s death. Caged Benthoctopus sp. in E2 moved frequently within the cage, particularly during the Live period (Fig. 5d), and appeared to attack its cell-mate 2 and 2.5 d after the start of the experiment. In these instances the octopus was in a feeding position with its arms around the macrourid (Fig. 3a). During the scavenging period, the Benthoctopus sp. apparently fed upon the carcass for a period of ~34 h, and then mostly clung to the top of the cage for the remainder of the time-lapse observations. Over this period the macrourids were skeletonized.

There is some indication that the caged Benthoctopus sp. and Coryphaenoides armatus avoided each other during E2. A Spearman’s rank correlation coefficient calculated for the position indices of the 2 species during the live period was –0.28 (p < 0.05). The correlation was positive (0.12), but non-significant, during the scavenging period, when the octopus was observed on the macrourid, apparently feeding, or at the top of the cage (Fig. 5).

Abundance and behavior of free-ranging scavengers

The abundance of scavengers and other benthos varied among phases and between experiments. Scavengers were observed during the live phase of E1 and E2, prior to the death of the caged macrourid, but were low in abundance compared to the scavenging phase. One exception to this pattern is the higher abundance of Coryphaenoides armatus at the beginning of E1, before its caged congener died (Fig. 6). Upon the death of the caged C. armatus in E1 and E2,
Fig. 5. *Coryphaenoides armatus*, *Pachycara bulbiceps* and *Benthocytalus* sp. Time series of scavenger activity inside cages. Low, mid, and high: the animal was observed in the bottom, middle, and upper third of the cage, respectively, for that image. Phases divided by dashed lines as in Fig. 4. E1: (a) *C. armatus* (Ind. 1 = , Ind. 2 = ) and (b) *P. bulbiceps* (n = 1). E2: (c) *C. armatus* (n = 1) and (d) *Benthocytalus* sp. (n = 1). Observations of apparent *Benthocytalus* attack on macrourid (live period) or apparent feeding on carcass by *Benthocytalus* (scavenging phase) ( ). For (b,c), ( ) represents a single individual.

Fig. 6. *Coryphaenoides armatus*, *Pachycara bulbiceps* and *Benthocytalus* sp. Abundance of scavengers during E1. Hours indicate the time from the death of the caged macrourid. Phases divided by dashed lines as in Fig. 4. (a) Number of *C. armatus* in images during the experiment. Note the lack of an increase in abundance following the death of the *C. armatus* individuals. (b) *P. bulbiceps* increased in frequency and abundance immediately following the death of the caged macrourids. (c) *Benthocytalus* sp. increased in frequency of occurrence for a period following the death of the macrourid.
the frequency of occurrence and abundance of the major scavengers increased, while visits by *C. armatus* to the cage decreased. During E2, scavengers, especially *Pachycara bulbiceps* and *Bassozetus nasus* (Ophidiidae), aggregated near the cage a few hours before the caged macrourid’s death, and then increased greatly following its demise (Fig. 7). *Benthoctopus* sp. and a small unidentified zoarcid species (possibly juvenile *P. bulbiceps*) also increased in response to the death of the macrourid, but were slower to arrive or increase in frequency near the cages, and reached peak abundances only after the number of *P. bulbiceps* and *B. nasus* waned. The strong response of scavengers is also evident by changes in the percentage of images with scavengers among periods (Table 2). Scavenging fishes were not able to feed on the macrourid carcasses because of their position within cages. *Benthoctopus* sp., however, could reach into the cage and pull the carcass to the cage margin for feeding. All scavengers were rare during the Consumed phase.

Correlation analyses used to assess interactions among scavengers suggested that *Benthoctopus* sp. and the unidentified small zoarcid may have avoided interactions with *Pachycara bulbiceps* and *B. nasus*. Spearman’s rank correlation coefficients for the abundance of *P. bulbiceps* or *B. nasus* and either *Benthoctopus* sp. or the unidentified zoarcid were not significant for the Live period. For the Scavenging period of E2, however, the abundance of the small zoarcid was negatively correlated to both *P. bulbiceps* (R = –0.20, p < 0.05) and *B. nasus* (R = –0.20, p < 0.05). In addition, the abundances of *Benthoctopus* sp. and *P. bulbiceps* were negatively correlated (R = –0.29, p < 0.05) during the Scavenging period.

A surprising result of the scavenger observations was the lack of response by macrourids in the vicinity to the death of the caged macrourids. *Coryphaenoides armatus* did not increase in abundance or frequency of occurrence following the death of their caged conspecifics (Figs. 6 & 7). Instead, *C. armatus* decreased in abundance and frequency upon the death of the caged macrourid during E1.

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**Fig. 7. Abundance of visiting scavengers during E2.** Hours indicate the time from the death of the caged macrourid. Phases divided by dashed lines as in Fig. 4. (a) *Coryphaenoides armatus*, (b) *Pachycara bulbiceps*, (c) *Bassozetus nasus*, (d) *Benthoctopus* sp., and (e) unknown zoarcid species. Note the shift in activity and visitation following the macrourid’s demise.
Common megafaunal invertebrates did not exhibit a strong response to the death of the macrourids. A few individuals of abyssal echinoids *Aporocidaris milleri* (Cidaridae), *Cystechinus loveni* (Urechinidae), and Ophiuroidea were observed in the camera view during all phases of E2, but did not change greatly in abundance between periods (Fig. 8). One *A. milleri* individual crawled slowly to the cage, but wandered out of view. Nor did *C. loveni* exhibit a response to the macrourid carcass. The buccinid gastropod *Mohnia vernalis* was observed occasionally. At least 1 *M. vernalis* was observed in successive images to crawl to the cage and onto the macrourid carcass. It is possible that others were present, but were obscured from view by the cage or other scavengers. Very low numbers of scavengers were observed during E3, which had no odor plume from caged fish, dead or alive. *Coryphaenoides armatus* was observed 5 times in ~100
images taken over ~200 h. Munnopsid isopods were the most abundant invertebrate, with 3 to 6 ind. visible in nearly all images. Benthic megafauna, including ophiuroids, holothurians, and gastropods (M. vernalis) were observed commonly as single individuals present in successive images as they wandered through the area, similar to observations in E2.

**DISCUSSION**

**Effects of ocean acidification on abyssal scavengers**

The potential effects of elevated ocean carbon dioxide levels include reduced calcification, respiratory stress, acid–base imbalance, metabolic depression, and potentially CO₂-induced torpor (Pörtner et al. 2004b, Raven et al. 2005). Although knowledge of the effects of high CO₂ tensions on deep-sea fishes is poor, tolerance is known to vary among species, perhaps related to their ability to control osmoles (Ishimatsu & Kita 1999, Ishimatsu et al. 2005). We have observed *Coryphaenoides armatus* to swim in very close proximity to pools of liquid CO₂, but their tolerance to long-term ocean acidification is unknown. CO₂-related stress may have contributed to the death of the caged macrourids positioned near CO₂ pools (n = 3 in these experiments), but this could not be evaluated, since all caged macrourids died, including those within cages at control sites with no CO₂ stress (n = 3). Unfortunately, it appears that mortality associated with cage-related stress was sufficiently high that all study animals died, precluding a comparison of survival rates for macrourids exposed to hypercapnic and normocapnic waters.

In contrast to *Coryphaenoides armatus*, all caged individuals of the zoarcid *Pachycara bulbiceps* and the octopus *Benthoctopus* sp. survived exposure at CO₂ treatment sites. *P. bulbiceps* was potentially exposed to the most severe stress due to its position on the seabed and the slightly negative buoyancy of the CO₂ dissolution plume. In addition, pH perturbations were likely larger during E1 for *P. bulbiceps* held in cages 0.5 m from the CO₂ pool. The pH sensors failed at this distance, but data from other experiments indicate that pH likely dropped by 1 U or more. Thus, *P. bulbiceps* is probably tolerant of more severe bouts of elevated CO₂ levels than indicated by the pH data presented here, which were collected 5 m from CO₂ pools. Overall, we placed 16 *P. bulbiceps* at distances from CO₂ pools of 0.5 to 5 m, where pH perturbations were episodic, but ranged from near –0.1 to >–1.0 U, and 6 ind. at control sites with no CO₂. All *P. bulbiceps* survived both month-long experiments. This confirms that the impaired physiological performance observed in cellular preparations of its shallower congener, *Pachycara brachycephalum*, during *in vitro* studies with pH perturbations near –0.6 U (Langenbuch & Pörtner 2003) does not characterize the sensitivity of the intact organism. Deep-sea cephalopods, including *Benthoctopus* sp., are known to be highly sensitive to even small changes in pH (Pörtner et al. 1998, Seibel & Walsh 2003). Thus, it is somewhat surprising that the caged *Benthoctopus* sp., as well as 2 others that have been in cages near CO₂ pools, survived the month-long period within the cage. Further studies are required to evaluate the metabolic costs of CO₂ tolerance and long-term consequences of increasing ocean acidification for deep-sea animals.

**Mortality of caged macrourids**

Death of macrourid fishes after 2 to 3 d within cages on the abyssal seabed was an unexpected, yet serendipitous event, providing an opportunity to observe the response of the abyssal scavenger assemblage, including conspecifics and congeners, to the odor plume following the caged macrourids’ deaths. Several factors may have contributed to their death, including the stress of confinement inside cages, increased exposure and interactions with potential predators (e.g. *Benthoctopus* sp., lysianassid amphipods), and the exposure to the CO₂-rich dissolution plume. Macrourids use a sensory barbel for gustation and mechanoreception while swimming in a somewhat head-down position (Bailey et al. 2007). This typical swimming behavior, along with their lack of experience with walls of any sort, may compromise their ability to detect the gaps in the cage mesh, leading to injury and death. Although each of these factors may have contributed, high mortality rates of caged macrourids have been observed by other investigators (Bailey et al. 2002).

**Response of scavengers to the macrourid odor plume**

The most striking result of the time-lapse observations was the indifference or possible avoidance of the odor plume by macrourids common at the study sites (mainly *Coryphaenoides armatus*). *C. armatus* was observed frequently at the study sites prior to the experiment and is a common scavenger at these depths.

Baited cameras in some areas and at some depths have not been visited heavily by macrourids. Macrourids were abundant in images at 1900 m, but were not observed at 4040 m over shark carcasses deployed in the Arabian Sea (Witte 1999). Results of video surveys at the sites largely mimicked those from the baited camera, with no macrourids observed at 4040 m depth. Thus, the local scavenger species pool did not include...
macrourids at Witte’s abyssal site. In contrast, Coryphaenoides armatus is one of the most abundant benthopelagic fishes at our study site, based on non-quantitative observations during ROV dive operations, and was readily captured in cages baited with mackerel.

At least 4 hypotheses may explain the avoidance or low response of Coryphaenoides armatus or other macrourids to the death of the caged C. armatus. First, grenadiers may have avoided the area due to the presence of the CO₂-rich dissolution plume. This explanation is not supported by the combination of pH and image data and ROV observations during the experiments. Macrourids were observed frequently during the initiation of the experiment and were the only scavenging fish to be observed near the CO₂ in E3, frequently swimming near CO₂ pools during ROV operations (J. Barry pers. obs.). Observations of the indifference exhibited by bathyal scavengers exposed to CO₂-rich seawater and odor plumes (Tamburri et al. 2000) also does not support this hypothesis. Although the CO₂-rich dissolution plume may have contributed to the death of the caged macrourid, this is not possible to evaluate since caged macrourids (2 in E1 and 1 in E2) positioned in control areas 50 to 100 m from CO₂ pools (where pH perturbations were undetectable) also died.

Second, macrourids may remain near food falls only in cases where access to the carcass is possible. The location of the macrourid carcass within the fish trap precluded feeding by macrourids visiting the cage. They may reduce risk of injury or death by leaving a site once they determine that feeding is difficult or impossible, regardless of the odor plume. This hypothesis is not supported by the observation of equal or fewer visits during the Live than Scavenging period in E2. It would require some period of time to assess feeding potential, an odor plume, if attractive, should result in higher attendance near the bait (and in images). The observed decrease in abundance of macrourids during the scavenging period tends to refute this hypothesis. The higher frequency of visits during the Live phase of E1 was likely related to the presence of some original bait remaining in the cage, which was not removed at the beginning of the experiment as in E2.

Third, the nutritional composition of the bait is likely to affect both the size and character of the odor plume, thereby influencing the response of the scavenger guild. It is possible that the odor plume from macrourids as bait is both smaller and less appealing to scavengers due to its lower lipid and protein concentrations, compared to those of shallow-water fishes or cetaceans. Depth-related trends in the composition of fish tissues have been reported by several investigators, but remain somewhat controversial. Bailey & Robison (1986) note a decrease in lipid, caloric, and protein content among fishes with depth. Closer examination of depth-related patterns among feeding type and position (i.e. benthic or benthopelagic) of demersal fishes revealed that the depth-related trends are coupled to mobility rather than food availability (Drazen 2007), with major changes in nutritional composition restricted largely to shallower, sunlit waters. Although the protein content of C. armatus tissue (15.6%) is high compared to that of most demersal fishes at bathyal and abyssal depths (Drazen 2007), it is lower than that found in fishes such as mackerel (~18%; Hardy & Keay 1972) or cetacean blubber (~60% [Aguilar & Borrel 1990]). Thus, the caloric density available to scavengers from C. armatus is clearly lower than that in studies using shallow-water species as bait, and may have contributed to the pattern of macrourid scavenging observed in the present study and in the study by Lampitt et al. (1983). On the contrary, however, other typical scavengers (liparids, ophidiids, octopods, zoarcids, lysianassids) appeared at baited cameras rapidly and abundantly in these studies, which does not support the hypothesis that the odor plume was deficient in some ways that would attract demersal scavengers.

Fourth, macrourids may either be unresponsive to or actively avoid the odor plume of conspecific or congeneric species. This could explain the reduced frequency of Coryphaenoides armatus observed during the Scavenging phase of E1 and the relatively constant number of macrourids observed throughout E2. We could find only 1 study (Lampitt et al. 1983) that used a macrourid (C. armatus) as bait for traps or camera studies of deep-sea scavengers. Their trap and camera deployments at the Porcupine Seabight in the North Atlantic attracted mainly lysianassid amphipods and the lipid fish Paraliparis bathybius. C. armatus was captured in the trap and was observed at the baited camera station, but in very low numbers. In contrast, camera systems baited with mackerel (Smith et al. 1997) or small cetaceans (Jones et al. 1998, Kemp et al. 2006) and deployed in the same area (23 to 315 km away) reported C. armatus as the overwhelmingly dominant scavenger. Collins et al. (1999) used bathyal toothfish Dissostichus eleginoides and squid as bait in camera systems deployed from 900 to 1750 m, in which toothfish visited the site, but did not consume either bait type. Other scavengers (hagfish, Myxinidae; stone crabs, Lithodidae; blue hake, Moridae; and amphipods) were much more abundant and consumed the
bait. Avoidance of conspecific odor plumes could confer a fitness advantage if it leads to higher survival, in spite of lost feeding opportunities at potentially dangerous sites. It is also possible that chemical releases from stressed, live animals, such as those held in cages during these experiments, could deter congeners from the area. Results from studies in shallow water, however, suggest that odors from conspecics often deter attendance near bait (Moore & Howarth 1996 and references therein).

Non-macrourid benthic and benthopelagic megafauna were common in time-lapse images and increased greatly in abundance immediately after the death of the caged macrourids. Like grenadiers, zoarcids and ophiidiids are common scavengers at deep-sea food falls in both the Pacific and Atlantic Ocean basins (Wilson & Smith 1984, Jones et al. 1998, Premke et al. 2003, Kemp et al. 2006). *Pachycara bulbiceps* is common near our study sites, based on ROV observations during the initiation of the experiments. It was observed frequently prior to the initiation of the experiments, and responded strongly to the death of *Coryphaenoides armatus*. *Bassozetus nasus* was observed several times during the Live period, but its response to the carcass lagged behind that of *P. bulbiceps* by several hours. It is possible that the odor plume was most intense near the seabed, where *P. bulbiceps*, a benthic species, would be more likely to encounter it than a benthopelagic species.

The pattern of visitation for *Pachycara bulbiceps* and *Bassozetus nasus* during the Scavenging period of E2 was somewhat contrary to expectations. The ophiidiid *B. nasus* is a benthopelagic fish that typically swims or hovers above the seabed. The zoarcid *P. bulbiceps* is benthic, and was usually motionless on the seabed. Assuming that it is principally a ‘sit and wait’ forager (Wilson & Smith 1984), due to its sedentary nature, its behavior near the cage would be expected to be similar to Bailey & Priede’s (2002) ‘sit and wait’ model (their Fig. 4). In their model, abundance rises rapidly to a peak, then drops abruptly following consumption of the bait. Instead, the pattern of visits for *P. bulbiceps* (Fig. 7) was much more similar to a cross-current foraging model (Priede et al. 1990, Bailey & Priede 2002), with a rapid rise in abundance and a rapid, but not precipitous, drop in abundance at the end of the scavenging period. Nor did *B. nasus* exhibit a pattern of abundance at the cage that was expected for its presumed foraging mode. Its benthopelagic mode suggests a cross-current foraging strategy, but its pattern of abundance (Fig. 7) more closely fits a ‘sit and wait’ model. Another consideration is the role of caged food falls in the area of the experiment, which could influence the pattern of scavenger visits at the camera location.

Changes in the relative abundance of scavengers suggest a successional sequence of exploitation, potentially driven by species-specific responses to the odor plume, interspecific interactions, or both. Successional changes in scavenger attendance at baited cameras have been detected for larger food falls, but rarely for small bait parcels consumed within hours. Owing to the long persistence and the heterogeneous resources available at whale falls, there is a well-documented succession of animals exploiting these sites (Smith et al. 2003). Smaller nekton falls can also have large effects on benthic communities, both from their role in carbon input as well as the physical disturbance to the seabed during active scavenging of the carcass (Smith 1985, 1986). Successional changes at food falls may also be motivated by predator avoidance or increases in predator abundance near aggregated prey (Smith 1985). Macrourids and liparids are known to consume lysianassid amphipods at food falls (Lampitt et al. 1983, Jones et al. 1998). Amphipods may be responsible for much of the consumption of some food falls, and fall prey to macrourids, liparids, zoarcids, or other predators. Typically, only large macrourids are photographed at bait (King et al. 2006), and only large specimens have carrion in their stomachs (Drazen et al. 2001), suggesting that small individuals are unable to compete for resources at food falls or actively avoid them due to predation risk. Ontogenetic increases in the size of the olfactory lobe of *Coryphaenoides armatus* indicate a shift from visual to olfactory cues (Wagner 2003), which may also influence the reduced response of small macrourids to odor plumes.

The Scavenging phase for macrourid carcasses in this study was considerably longer than has been observed in various other studies when a single mackerel was used for bait. We assume this is due to the limited access by megafaunal scavengers. The *Benthotopus* sp. inside the cage had direct access to the macrourid carcass in E1 and appeared to feed upon it during the scavenging period, apparently moving the carcass within the cage. Other *Benthotopus* sp. visiting the cage were observed to reach into the cage, apparently pulling the carcass toward them so that they may feed on it. Amphipods, sampled poorly by this study, had the greatest access to the carcass, and very likely consumed a significant portion of the carcass, as well as being fed upon by other scavengers.
Although our observations of scavenger responses to the macrourid odor plume support the hypothesis of aversion to odors from injured or dead conspecifics, our experiments were not designed to evaluate this hypothesis. Our test of this hypothesis lacks adequate controls, and the effects of odor plumes are confounded with those caused by the CO₂-rich dissolution plume from nearby CO₂ pools. Future studies of scavenger behavior should include observations of scavenger responses at several sites with and without macrourid bait, and in the absence of CO₂-laden waters. Integration of our understanding of factors influencing scavenger behavior with information concerning the impacts of exposure to CO₂-enriched waters will increase our abilities to forecast changes in deep-sea ecosystems under future changes in ocean chemistry.

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LITERATURE CITED


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Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations

Mike Cappo1,2,*, Glenn De’ath1, Peter Speare1

1Australian Institute of Marine Science, PMB 3, Townsville MC, Queensland 4810, Australia
2School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia

ABSTRACT: A fleet of baited remote underwater video stations was set in lagoonal and inter-reef waters of the Great Barrier Reef Marine Park, across 14° of latitude and the entire shelf. Counts of the maximum number seen in any one field of view were used to estimate relative abundance of 347 species of bony fishes, cartilaginous fishes and sea snakes. Boosted regression trees were used to assess the influence of depth and location of sampling sites on species richness. Multivariate regression trees and indices of specificity and fidelity (Dufrêne-Legendre indices) were used to distinguish 17 spatially contiguous vertebrate groups within a hierarchy of spatial scales. Location across the shelf and depth had the greatest influence on species richness, with peaks occurring around the ~35 m isobath in the inter-reef waters of the reef matrix, coinciding with shallow banks and shoals. Richness increased slightly toward the equator. Nine terminal vertebrate communities parallel to the coast were distinguished inshore and offshore in deep and shallow water along a latitudinal gradient. There were important community boundaries at Bowen in the south, Townsville in the centre, and Cape Flattery in the north. Latitudinal groupings were most evident inshore. Offshore communities were spatially extensive and separated lagoonal, mid-shelf and outer-shelf sites. Community boundaries were correlated with knowledge of strong gradients in sedimentary and oceanographic processes influenced by the shape of the reef matrix and regional tides and currents.

KEY WORDS: Underwater baited video · Inter-reef · Demersal fish communities · Multivariate regression trees

INTRODUCTION

In the tropics, the biodiversity of shallow-water coral reefs has been the focus of concern and research, yet much of the world’s coral is found on shelf areas in benthic communities that are non-emergent and often 10s of metres below the surface (McManus 1997, Spalding & Grenfell 1997). These ‘live bottom’ communities occur on coarse sediments, palaeo-reef edges, or other outcrops and include sponges, gorgonians, alcyonarians, corals and marine plants in a wide variety of sizes and densities (Birtles & Arnold 1988, McManus 1997, Carruthers et al. 2002). Such habitats are undoubtedly a major, but poorly known, reservoir of marine biodiversity, and their structural complexity provides habitat for a variety of other species. In some regions they have been fished intensively enough to produce changes in compositions of fish (Sainsbury et al. 1997, Laurans et al. 2004) and megazoobenthos communities (Pitcher et al. 2000).

The deeper habitats are inaccessible to the SCUBA-based survey techniques developed for shallow-water reefs, and baited ‘video-fishing’ techniques have recently been used alone or in association with other methods to count fishes (Ellis & DeMartini 1995, Willis et al. 2000). Such non-extractive video techniques offer the sampling advantages of underwater visual surveys and extractive fishing techniques, whilst avoiding some of the selectivity associated with these methods (see Willis et al. 2000, Cappo et al. 2003 for reviews).
A comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls showed that the 2 techniques recorded significantly different components of the fish fauna in the Great Barrier Reef Marine Park (GBRMP) lagoon, yet both discriminated amongst the same site groups (Cappo et al. 2004). Trawls caught mainly small (≤300 mm), sedentary, or cryptic, demersal species. The BRUVS recorded larger, mobile species from a much wider size range of families, and BRUVS were subsequently included in the suite of sampling devices used in the most comprehensive exploration of seafloor biodiversity yet undertaken in the GBRMP (Pitcher et al. 2002).

In the present paper we examine the relative influence of water depth and position across and along the GBRMP shelf on vertebrate species richness and community structure, as a prelude to a more intensive analysis of other biotic and abiotic explanatory variables. We use boosted and multivariate regression trees (De’ath 2002, 2007) and species accumulation curves to describe patterns in the richness, occurrence and abundance of fishes, sharks, rays and sea snakes sighted in standardised BRUVS surveys. The trees were used to define spatially contiguous vertebrate communities constrained by the spatial values that locate them in the GBRMP.

MATERIALS AND METHODS

Study area and sampling design. The GBRMP is the largest coral reef ecosystem on earth, with an interreef area of 210,000 km², extending over 2000 km of coastline and 15° of latitude in an approximately northwest–southeast direction (Fig. 1). The lip of the GBR shelf occurs at only 80 m depth, and the shelf plain has a very flat seaward gradient <1:1000 (Larcombe & Carter 2004). Biologically informed stratification of major physical variables was used to sample as many different habitat types as possible in the ‘environment space’ of the GBRMP (see Pitcher et al. 2002). Between September 2003 and December 2005, a fleet of BRUVS was deployed during daylight hours about 350 to 400 m apart, with the prevailing wind to bracket the coordinate of each sampling site. Each replicate was considered to be independent of the others at this distance of separation (Cappo et al. 2004). At each site, a stereo-video BRUVS was deployed first, followed by 3 (97% of sites) or occasionally 4 BRUVS with single cameras. Loss of some replicates was made up to a minimum number of 3 for the 366 sites by inclusion of footage from the stereo-video (Fig. 1).

The BRUVS consisted of a galvanized, trestle-shaped frame, enclosing a simple camera housing made from PVC pipe with acrylic front and rear ports (Fig. 2). Sony Mini-DV HandiCams (Models TRV18E, TRV19E) with wide-angle lens adapters (0.6×) were used in the housings. Exposure was set to ‘Auto’, focus was set to ‘Infinity/Manual’, and ‘Standard Play’ mode was selected to provide at least 45 min of filming at the seabed (mean ± SD; 53.3 ± 11.3 min). Detachable bait arms (20 mm plastic conduit) had a 350 mm plastic...
mesh canister containing 1 kg of crushed oily sardines (*Sardinops or Sardinella* spp.) as bait, lying on the seabed (Fig. 2). BRUVS were deployed with 8 mm polypropylene ropes and polystyrene surface floats bearing a marker flag, and were retrieved with an hydraulic pot-hauler wheel.

Interrogation of each tape was conducted using a custom interface (BRUVS1.5.mdb, Australian Institute of Marine Science, 2006) to manage data from field operations and tape reading, to capture the timing of events and to capture reference images of the seafloor and fish in the field of view. Records were made for each species of the maximum number seen together at any one time on the whole tape (MaxN). The use of MaxN as an estimator of relative abundance has been reviewed in detail by Cappo et al. (2003, 2004). Species identifications were confirmed by checking the collection of reference images with taxonomists, and 14% of the records were subsequently pooled in ‘taxa’ at the level of species group, genus, family, or order. These taxa are hereafter referred to as species. Data were analysed at the level of individual sites by summing the replicate MaxN for each species and transforming them by fourth root. The ‘locations’ of the sites were defined by mean depth and relative distance across and along the GBRMP (Fabricius & De’ath 2001). Distance across was set to the value 0 on the coast and 1 on the outermost edge of the continental shelf (80 m isobath), and distance along the shelf takes the value 0 on the southern edge of the GBRMP and 1 on the northern edge (Fig. 3).

**Data analysis.** The dependence of site richness on location and depth was assessed using boosted trees (Friedman 2001, Leathwick et al. 2006, De’ath 2007). The transformed estimates of relative abundance (MaxN) of the observed species were analysed using multivariate regression trees (MRT; De’ath 2002). Dufrêne-Legendre index values (DLI; Dufrêne & Legendre 1997) were then calculated for each species for each node of the tree. For each species and group of sites, the DLI is defined as the product of the mean species abundance occurring in the group divided by the sum of the mean abundances in all other groups, times the proportion of sites within the group where the species occurs, multiplied by 100. Each species was associated with the tree node where its maximum DLI value occurred. High DLI values were used to characterise representatives of each community, and the spatial extent of the group indicated the region where the species was predominantly found (see DeVantier et al. 2006 for further details). All analyses used the R statistical package (R Development Core Team 2005), including the packages gbm, fields, mvpart and vegan.

**RESULTS**

The final dataset consisted of 366 sites and 39,989 individuals from 347 species of vertebrates. The bony fishes were from 10 Orders, dominated by Perciformes (267 species), Tetraodontiformes (27), Anguilliformes (6), Aulopiformes (3), Scorpaeniformes, Clupeiformes, Beryciformes with 2 species, and Siluriformes, Pleuronectiformes and Gasterosteiformes each with a single species. The chondrichthyians were well represented by the Carcharhiniformes (15 species), Rajiformes (13) and Orectolobiformes (3). There were 5 species of sea snakes from the Family Hydrophiidae.

**Species richness**

There was an average (±SD) of 13.8 ± 6 species site⁻¹, ranging from 2 to 43. Most vertebrates were rare or uncommon, occurring in only a very small percentage of the sites surveyed. Ordering of the most diverse sites produced a sigmoidal curve (Fig. 4a), showing ~14% of sites had comparatively high species richness (≥20 species), ~41% had moderate richness (≥13 species), and 18% had relatively low richness (≤8 species). Just over 90% of the species were recorded in <10% of the sites, and ~43% were recorded only 1 to 3 times (Fig. 4b). Only ~5% of the species were moderately prevalent, occurring in ≥20% of the sites, and only *Nemipterus turcosus* had a prevalence >50%. General patterns in species richness interpolated by latitude and longitude showed that cross-shelf and along-shore gradients were not simple (see Fig. 8a). Higher richness occurred at sites in the outer reef matrix, particularly north of Proserpine (20° S), with a ‘hotspot’ off Cape Flattery (15° S) in the far north. Richness in the
southern half of the GBRMP was higher around the Capricorn-Bunker (23.5° S) island group, and consistently lower for the coastal bays, the deep mid-shelf waters of the Capricorn trough (≥22.5° S), and the inter-reef waters of the outer barrier reefs (see Fig. 8a).

Cross-shelf position and depth had the greatest influence on richness, which increased monotonically in response to relative distance along the shelf from the southern boundary (Fig. 5). Richness increased across the shelf, with a sharp peak occurring at ~0.8, where sites had ~3 more species on average than elsewhere. This isopleth coincides with the mid-shelf reef matrix south of Cardwell (18.25° S) and the outer barrier reef north of Cardwell (Fig. 3). A modal relationship showed peak richness for depths in the 30 to 35 m range (Fig. 5d), in the lagoon and on the
banks and shoals amongst the reef matrix (Fig. 3). The average decline in richness beyond depths of ~35 m was about 0.1 species m\(^{-1}\).

The first-order interactions showed that cross-shelf increase in richness was most pronounced for shallower sites ~35 m, but the peak in richness at ~0.8 occurred for all depths. There was a slight decline in richness with increasing distance across the shelf for sites deeper than 50 m (Fig. 6a). The decline in richness for depths >35 m was most pronounced for sites at cross-shelf positions offshore from ~0.6, coinciding with the inner edge of the reef matrix south of Cardwell and the offshore reef matrix north of Cardwell (Fig. 3). There was also a considerably higher rate of northward increase in species richness at sites within the inter-reef waters ~0.8 across the shelf (Fig. 6b).

**Patterns in vertebrate communities**

Hierarchical vertebrate communities were defined by MRT constrained by location and depth of the sites. A tree with 9 terminal nodes was selected to represent the most parsimonious community structure in similar species composition (Fig. 7). The tree explained 28% of the variation in the transformed species abundance data—not unusual for datasets containing large numbers of species occurring with low abundance (DeVantier et al. 2006).
The primary split separated inshore and offshore groups at ~0.5 half-way across the shelf. This isopleth lies in the open waters of the lagoon in the southern half of the GBRMP, south of Cardwell, and in the reef matrix in the northern half. The next splits distinguished shallow and deep groupings on either side of the ~36 m isobath within each of these regions. Within the inshore side of the tree, the lower level splits were all based on distances along the shelf. The inshore node split into groups north and south of Cape Flattery (along ~0.74), with 4 terminal groups north and south of the top of the Whitsunday islands, near Bowen (20°S) (along ~0.37). The offshore side of the tree included nodes separating the deeper sites amongst

Fig. 6. Partial dependency of site species richness at 5 distances across the shelf (a) on depth and (b) on the distance along the shelf. Other conventions described in Fig. 5

Fig. 7. Multivariate regression tree analysis defining transformed relative abundance of vertebrate communities in terms of location and depth. The terminal nodes represent 9 communities inshore (In) and offshore (Off) in the far north (FN), north (N), central (C), south (S), shallow (Sh), deep (Dp), lagoon (Lag), mid-shelf (Mid) and inter-reef (Rf) regions (see Fig. 8 for locations). The higher level nodes represent the 8 communities at higher spatial scales in these regions. The bar plots show the distribution of mean species abundances at each of the terminal nodes, ranked from left to right in decreasing order of prevalence in the entire dataset, with the number of sites within each group (n). Species richness in terminal groups is shown next to the number of indicator species, with maximum Dufrêne-Legendre index values in brackets.
the reef matrix north and south of Magnetic Passage
off Townsville (18.5° S) (along ~0.48), and north and
south of Port Douglas (16.5° S) (along ~0.65) at depths
of <36 m.

The location of BRUVS sites within the 9 terminal tree
groupings was described by deep and shallow groupings
in the far north (FN), central (C) and southern (S) regions
of the GBRMP. Within these regions the lagoon (Lag),
mid-shelf (Mid) and inter-reef (Rf) waters of the reef ma-
trix can be recognised (Fig. 8b,c). Latitudinal variation
was greatest inshore in the lagoon, with 3 shallow com-
munities separated in the north off Cape Flattery and in
the south off Bowen (FN-Mid-Sh, C-Lag-Sh, S-Lag-Sh),
and 2 deep lagoon communities on either side of Bowen
(S-Lag-Dp, NC-Mid-Dp). Sites in the groups offshore
amongst the reef matrix also split based on the location
along the shelf. Shallow-water groups occurred on
shaos and banks in the reef matrix, north of Cape Flatt-
tery (FN-Off-Sh) and south of Cairns (S-Rf-Sh). Deeper
sites in the passages and plains between the reefs split

Fig. 8. Model of (a) species richness interpolated for the study area (rotated) with a smoothed thin plate spline technique and
(b,c) location of sites within the 9 vertebrate community groups divided into shallow and deep groups within regions of the
GBRMP (rotated). See Fig. 7 for community abbreviations
into 2 extensive offshore groups north (N-Rf-Dp) and south (S-Rf-Dp) of Magnetic Passage off Townsville.

Most species were rare in each group, but the majority of the few prevalent species had consistently higher abundances in the 2 shallow offshore groups (FN-Off-Sh and S-Rf-Sh) (Fig. 7). Less than 3% of species had a high DLI (≥50), and most of these occurred in 4 dominant, higher level community nodes (Tables 1 & 2, Fig. 7). Only 12% of species had moderately high DLI values (between 20 and 50), and more than half of these occurred in the terminal groups, most notably the offshore, shallow nodes. There were only 29 sites (8%) in the S-Rf-Sh and FN-Off-Sh groups, yet they dominated the analysis of DLI values for >36% of all species (Fig. 7), mostly in the families known to associate with complex seabed topography (Table 2). In contrast, C-Lag-Sh and S-Rf-Dp contained no indicator species with moderate values. The largest terminal group (S-Rf-Dp) in the tree had 28% of the sites and 47% of the recorded species, yet abundances were generally very low and none had moderately high DLI values there. Such groups were dominated by others in spatial hierarchy, in the sense that all their species members also occurred in higher numbers elsewhere. The 17 indicator species with DLI maxima at the root node were generally ubiquitous, abundant and widely distributed (Table 1).

The most striking groupings were S-Rf-Sh and FN-Off-Sh, within the shallow offshore side of the tree—comprising only 8% of all sites, but including >51% of all species and DLI maxima for >31% of all species. Sites in these communities had the highest richness and higher abundance than most other terminal groups (Table 2). Species accumulation curves in these 2 moderately rich communities showed the fastest rates of increase and no sign of reaching an asymptote (Fig. 9). The richest community (N-Rf-Dp) comprising a moderate number of sites also had a relatively high rate of species accumulation. The other 7 communities showed lower species accumulation rates, and only the group with the largest number of sites (S-Rf-Dp) showed strong curvature toward an asymptote in species richness (Fig. 9). These trends indicate that the sampling effort had not produced a comprehensive representation of species diversity within most of the communities.

**DISCUSSION**

Significant ecological differences have been reported in the GBRMP, along the strong cross-shelf gradients readily measurable in riverine outflow, nutrient input, water clarity and exposure to prevailing wind and waves (e.g. Wilkinson & Cheshire 1988, Newman et al. 1997, Drew 2001). Few studies have incorporated the latitudinal gradient along the shelf (Williams 1991, Fabricius & De’ath 2001, DeVantier et al. 2006), and most have been restricted to the depth limits of SCUBA diving observations on shallow reefs. The results reported here

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Table 1. Summaries of richness in the 8 higher order fish communities. Details of all species with moderate to high values of the Dufrêne-Legendre index (DLI ≥ 20), or only the top 5 indicator species, within each site group are shown with DLI in parentheses. For a given species and a given group of sites, the DLI is defined as the product of the mean species abundance occurring in the group divided by the sum of the mean abundances in all other groups (specificity), multiplied by the proportion of sites within the group where the species occurs (fidelity), multiplied by 100. See Fig. 7 for community abbreviations.

<table>
<thead>
<tr>
<th>Node no. / grouping</th>
<th>No. of sites (species)</th>
<th>Indicator species (DLI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 All</td>
<td>366 (347)</td>
<td>Nemipterus furcosus (52), Echeneis naucrates (47), Abalistes stellatus (40), Pentapodus paradiseus (37), Lagocephalus sceleratus (34), Carangoides fulvoguttatus (27)</td>
</tr>
<tr>
<td>2 In</td>
<td>196 (187)</td>
<td>Scomberomorus queenslandicus (64), Selaroides leptolepis (56), Nemipterus hexodon (40), Carangoides coerulopinna (34), Gymnothorax minor (29), Nemipterus peronii (21)</td>
</tr>
<tr>
<td>3 Off</td>
<td>170 (295)</td>
<td>Pentapodus nagasakienis (51), Lutjanus sebae (15), Parupeneus heptacanthus (14), Pristis obtusirostris (14), Galeocerdo cuvier (10), Loxodon macrorhinos (10)</td>
</tr>
<tr>
<td>4 In-Sh</td>
<td>134 (167)</td>
<td>Paramonacanthus oitensis (36), Carangoides hedlandensis (21), Lutjanus carponotatus (2)</td>
</tr>
<tr>
<td>5 In-Dp</td>
<td>62 (124)</td>
<td>Nemipterus theodori (53), Seriolina nigrofasciata (51), Saurida grp. (43), Decapterus russelli (38), Lutjanus malabaricus (10)</td>
</tr>
<tr>
<td>6 Off-Dp</td>
<td>141 (256)</td>
<td>Cararchinus albimarginatus (12), Pleuronectiformes grp. (7), Arrothron stellatus (3), Pentapodus sp. (3), Chaetodon auriga (2)</td>
</tr>
<tr>
<td>7 Off-Sh</td>
<td>29 (177)</td>
<td>Parupeneus aureofasciatus (38), Parupeneus barberinoides (36), Symphorus nematophorus (35), Lethrinus genivittatus (31), Lethrinus semincinctus (28), Upenue tragula grp. (25), Gnathanodon speciosus (24), Nebrius ferrugineus (22)</td>
</tr>
<tr>
<td>8 CS-In-Sh</td>
<td>99 (151)</td>
<td>Herklotsichthys lippa (2), Pomadasys kaakan (2)</td>
</tr>
</tbody>
</table>
are the first attempt at describing the patterns in vertebrate communities in terms of both the horizontal cross-shelf and along-shelf gradients and the third, vertical dimension of the full range of shelf depths.

The use of boosted and multivariate regression trees has provided compelling results concerning the cross-shelf rise in species richness in the lagoon and amongst the reef matrix, the existence of spatially contiguous

Table 2. Summaries of mean, standard deviation and range of richness and abundance (abund.) in the 9 terminal fish communities. Details of species with moderate to high values of the Dufrêne-Legendre index (DLI ≥ 20), or only the top 5 indicator species, within each site group are shown with DLI in brackets. See Fig. 7 for community abbreviations.

<table>
<thead>
<tr>
<th>Node no./ grouping</th>
<th>No. of sites (species)</th>
<th>Richness: mean ± SD (range)</th>
<th>Raw abund.: mean ± SD (range)</th>
<th>Indicator species (DLI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 NC-Mid-Dp</td>
<td>21 (81)</td>
<td>14.5 ± 2.9 (8 to 21)</td>
<td>197 ± 326 (19 to 1485)</td>
<td>Scolopsis taeniopus (21), Aiptypurus laevis (20), Nemipterus nematopus (15), Paramonacanthus lowei (14), Sphyraena jello (8)</td>
</tr>
<tr>
<td>11 S-Lag-D</td>
<td>41 (105)</td>
<td>15.4 ± 4.6 (8 to 26)</td>
<td>115 ± 56 (39 to 233)</td>
<td>Paramonacanthus filicauda (63), Carangoides malabaricus grp. (28), Caranx bucculentus (18), Terapon jarbua (12), Pristipomoides multidens (8)</td>
</tr>
<tr>
<td>12 S-Rf-Dp</td>
<td>104 (165)</td>
<td>11.8 ± 5.3 (3 to 29)</td>
<td>93 ± 75 (10 to 585)</td>
<td>Upeneus fliifer (11), Oxycyelixus celebicus (4), Halichoeres sp. (4), Thalassoma ambycephalum (3), Coris picta (3)</td>
</tr>
<tr>
<td>13 N-Rf-Dp</td>
<td>37 (186)</td>
<td>15.7 ± 8.3 (3 to 42)</td>
<td>63 ± 29 (19 to 155)</td>
<td>Gymnomranius granuloculis (26), Nemipterus balinensisoides grp. (17), Pristipomoides typus (14), Lutjanus bohar (11), Epinephelus cyanopodus (11)</td>
</tr>
<tr>
<td>9 FN-Mid-Sh</td>
<td>35 (85)</td>
<td>14.7 ± 3.4 (8 to 23)</td>
<td>183 ± 219 (60 to 1290)</td>
<td>Atule mate (26), Carcharhinus tilstoni grp. (23) Alepes aperca (23), Lagoscephalus grp. (13), Choerodon cephalotes (10)</td>
</tr>
<tr>
<td>14 FN-Off-Sh</td>
<td>15 (98)</td>
<td>19.3 ± 6 (6 to 28)</td>
<td>164 ± 129 (25 to 525)</td>
<td>Amblypmacentrurus breviceps (66), Oxycyelixus himaculatus (56), Paramonacanthus japonicus (54), Apiron virescens (20), Himantura iai grp. (20), Meiacanthus grammistes (20), Choerodon gomoni (20)</td>
</tr>
<tr>
<td>15 S-Rf-Sh</td>
<td>14 (132)</td>
<td>22.9 ± 9.1 (10 to 43)</td>
<td>127 ± 77 (25 to 262)</td>
<td>Choerodon venustus (48), Lethrinus miniatus (48), Parapercis xanthozona grp. (48), Pomacentrus nagasakienesis (44), Lethrinus rarus (43), Pomacentrus australis (39), Gymnomranius audleyi (32), Chaetodontoplus meridithi (32), Plectropomus leopardus (23), Chrysipera rolandii (21)</td>
</tr>
<tr>
<td>16 S-Lag-Sh</td>
<td>40 (90)</td>
<td>10.4 ± 3.9 (2 to 21)</td>
<td>74 ± 63 (17 to 355)</td>
<td>Platyccephalidae grp. (22), Pomadasys maculatus (5), Silago grp. (3), Aluterus monoceros (3), Chaetodontopus doubolayi (3)</td>
</tr>
<tr>
<td>17 C-Lag-Sh</td>
<td>59 (123)</td>
<td>12.8 ± 4.8 (4 to 28)</td>
<td>94 ± 146 (6 to 1096)</td>
<td>Carangoidea talamaporoides grp. (13), Lepomis hardwickei (9), Apogon kienisi (2), Epinephelus malabaricus (2), Heniochus acuminatus (2)</td>
</tr>
</tbody>
</table>

Fig. 9. Species-accumulation curves for the (a) 4 deep and (b) 5 shallow regional communities. See Fig. 7 for community abbreviations.
vertebrate communities along and across the shelf, and
the existence of community boundaries near Bowen
(20°S) in the south, Townsville (18.5°S) in the central
section, and Port Douglas (16.5°S) and Cape Flattery
(15°S) in the north. These robust patterns were
detected amongst a functionally diverse cross-section
of the aquatic vertebrate fauna by a simple, efficient
baited video technique without disturbing seafloor
habitats or harming the fauna.

Spatial trends in species richness

Cross-shelf position and depth had the greatest
influence in predicting species richness, which
increased with distance across the shelf to a sharp
peak, ~0.8 where coral reefs exist and sites had about
4 species above average. A modal relationship pre-
dicted peak richness for depths in the 30 to 35 m range,
in the lagoon and banks and shoals amongst the reef
matrix, followed by a decline of about 1 species for
each 10 m increase in depth. The position of this iso-
bath across the shelf varied as the lagoon and reef
matrix generally taper in width from south to north.
The habitats at these depths are poorly known, but
include vast Halimeda algal banks (Drew 2001) and
deep-water seagrass in the lagoon (Carruthers et al.
2002). The weak northward increase in species rich-
ness of about 1 species for every 3° of latitude was
expected, given general patterns in aquatic species
diversity (Gray 2001) and previous studies in the
GBRMP (DeVantier et al. 2006). The interactions
amongst the northward, cross-shelf rise in richness and
the modal influence of depth indicated lower diversity
for a given depth in the deeper gutters, passages and
inter-reef plains between the reefs.

It is possible that mid-shelf peaks in species richness
might arise through simple geometric overlap of range
boundaries of nearshore and offshore species assem-
blages in the absence of any environmental gradients.
This is termed the ‘mid-domain effect’ (Colwell et al.
2004), and might explain why highest richness was
interpolated for the localised region offshore of Cape
Flattery, where sampling sites in close proximity were
separated into 5 species communities.

Most species were rare and species accumulation
curves approached an asymptote for only a single
community group, implying that full representation
of the diversity of most communities will require more
sampling. The richer communities had low inflection
points on the ordinate axis and a long upward slope
toward an asymptote—a curve shape characteristic of
faunas with a high proportion of rare species and a
few abundant species (Magurran & Henderson 2003,
Thompson & Withers 2003). This pattern seems charac-
teristic of tropical fish faunas sampled by trawl, as Stobutzki et al. (2001) found that 75% of species occurred
in <10% of prawn trawls, and Blaber et al. (1994) found
that 75% of the biomass in fish trawls was composed of
only 8% of the species caught. Like estuarine fish
faunas (Magurran & Henderson 2003), the vertebrates
in the inter-reef waters of the GBRMP probably com-
prise ‘core species’, which are persistent, abundant
and biologically associated with particular habitats,
and ‘occasional species’, which occur infrequently in
surveys, are typically low in abundance and have
different habitat requirements.

Shelf-scale patterns in vertebrate communities

The multivariate trees were used to define a hierar-
chy of groups of species that co-occur at varying spatial
scales to form communities. This contrasts with non-
hierarchical methods (such as K-means clustering),
which derive mutually exclusive clusters at a single
spatial scale, thereby lacking information at broad
spatial scales and not highlighting information from
highly prevalent species (De’ath 2007).

Shallow and deep communities on either side of the
~35 m isobath were distinguished along strong cross-
shelf and latitudinal gradients. Latitudinal variation
was greatest in the inner half of the shelf, where
Bowen and Cape Flattery separated 3 shallow inner-
shelf groups and 2 deep mid-shelf communities. The
offshore communities were latitudinally more exten-
sive, but still split into a northern and a southern
group, showing that outer-shelf deep communities
were more similar amongst latitudes than to mid-shelf
depth communities at the same latitude and vice versa.
The mid-shelf sites north of Cape Flattery showed
closer similarity to the nearshore sites to the south
than they did to the mid-shelf sites elsewhere. Both these
trends were similar to the patterns found by Williams
(1991) for coral reef fish communities, for which mid-
shelf reefs in the far north were more similar to
nearshore reefs elsewhere than to mid-shelf reefs at
more southerly latitudes.

Cross-shelf gradients in tropical, demersal fish com-
}
shelf occurrence of different families, and single families often contained a number of species that characterised different communities.

Ubiquitous families such as the nemipterids, monacanthids, carcharhinids and tetraodontids had representatives in both inshore and offshore, deep and shallow communities. The inshore community included many indicator species from the ‘small pelagic’ functional groups, such as the piscivorous Scomberomorus and small zooplanktivorous carangids (Alepes, Atule, Selaroides and Carangoides). Hydrophid sea snakes, and demersal teraponids and bathysaurids, were also characteristic of inshore groups and are known to inhabit soft sediments elsewhere in the Indo-Pacific (Blaber et al. 1994, Sainsbury et al. 1997). Indicator species offshore included many representatives of the lutjanids, lethriniids, pomacentrids, dasyatids, mullid, pinguiipedids and serranids known to be associated with more complex seafloor topography, such as reefs, rocks and rubble. Deep-water lutjanids and serranids (Pristipomoides, Epinephelus) characterised communities where the deepest water occurred.

**Cross-shelf and latitudinal gradients in the GBRMP**

We propose that cross-shelf variation in sedimentary processes and along-shelf variability in oceanic influences shape the boundaries identified here amongst communities. The wide range of inter-reef habitats is dominated in different regions of the GBRMP by combinations of cyclonic events, tides, currents and upwellings, waves, riverine inputs and seasonal winds (Larcombe & Carter 2004, Porter-Smith et al. 2004). These forces govern the topography, grain size and composition of sediments, the chemical properties of overlying waters and therefore the nature of infaunal, phototrophic or filter-feeding epibenthic communities (e.g. Birtles & Arnold 1988). In turn, these habitats influence the recruitment, feeding success and mortality of the fish communities inhabiting them (Sainsbury et al. 1997).

There were 3 broad cross-shelf zones in location of the vertebrate communities (Lag, Mid, Off) that can be related in the region south of Cape Flattery to 3 sedimentary belts in seabed composition and topography described by Larcombe & Carter (2004). They defined a terrigenous prism of bioturbated sand and mud extending to depths of 20 to 22 m, a lagoonal zone (22 to 40 m) with mixed shelly, muddy sand and shell hash overlying weathered Pleistocene clay, and an inter-reef zone (40 to 80 m), starved of terrigenous sediment, where there are Pleistocene reef remnants amongst detrital carbonate sediments. These zones are maintained through the influence of south-easterly trade winds driving along-shelf drift northward, and by the regular passage of tropical cyclones causing strong northward currents in the lagoon.

The clear latitudinal boundaries between the communities at Bowen, Townsville and Cape Flattery can be related to the configuration of the shelf and reef matrix, currents and tides. Much of the area south of Bowen is macrotidal (to 8.2 m near 22°S), and Porter-Smith et al. (2004) predicted that mobility and grain size properties of the sediment in this region were dominated by tidal currents, in contrast with the rest of the GBRMP. Deep-water seagrasses (mainly Halophila spp.) are known to respond to these gradients. They were reported by Carruthers et al. (2002) to be absent from most of the ‘tide-only’ region south of Bowen, and to be uncommon north of Cape Flattery, where nutrient or recruitment limitation restricts their abundance. The beds of highest density are known to occur mostly on the inner shelf of the central GBRMP in 15 to 58 m (Carruthers et al. 2002). Meadows of the alga Halimedea also occur in clear waters, but their richest development, into extensive, 15 to 20 m thick bioherms, is driven by tidal jetting of nutrients behind the chain of Ribbon reefs north of Port Douglas (Drew 2001).

The westward impingement and bifurcation of the South Equatorial Current (SEC) against the continental shelf peaks in the central region (14 to 20°S), providing a further explanation for our community boundaries at Bowen and Cape Flattery. The reef matrix is significantly more ‘permeable’ in this central section between the Ribbon reefs in the north and the Pompey reefs off Proserpine to the south. The density of barrier reefs is much lower, and the westward flowing SEC readily traverses the numerous passages shoreward in this central region. This direct infiltration of the SEC, as well as regional upwelling induced by the southerly setting East Australian Current (Wolanski 1994), drives an influx of oceanic water across the reef matrix as far as the mid-shelf. The northward flow in the lagoon induced by the trade winds effectively halts this influx, forming a coastal boundary layer (Brinkman et al. 2002). The result is a cross-shelf gradient that isolates nearshore waters from the outer lagoon in the central section, and the formation of 3 different regions of water movement along the GBRMP.

There are also latitudinal gradients in flushing rates and the amplitude of seasonal variation in sea-surface temperature (SST) and salinity. Hancock et al. (2006) found that inner lagoon diffusivity was about 2.5 times higher in the central section compared to in the north, so that water within 20 km of the coast is flushed with outer lagoon water on a time scale of 18 to 45 d, with the flushing time increasing northwards. Salinities in the southern lagoon are significantly higher than those in the central and northern sections, and seasonal vari-
ation is lower. Summer SSTs are ~2 to 3°C lower in the region south of Bowen compared to in the region to the far north, and in winter a relatively cold coastal water body forms there (Condie & Dunn 2006).

CONCLUSIONS

The cross-shelf layers we describe in species richness and community groupings fit well with knowledge of gradients and boundaries in sedimentary processes and water circulation patterns in a cooler, macrotidal southern region, a well-flushed central region, and a warmer, constricted northern region. The next step is to analyse these spatial factors with a comprehensive suite of physical and biotic covariates to refine definition of the shelf-scale patterns in communities and their indicator species and to predict their underlying influences.

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How to estimate scavenger fish abundance using baited camera data

K. D. Farnsworth1,*, U. H. Thygesen2, S. Ditlevsen3, N. J. King4

1School of Biological Science, Queens University Belfast, 97 Lisburn Road, Belfast BT9 7BL, UK
2Danmarks Fiskeriundersøgelser Afd. for Havfiskeri, Charlottenlund Slot, 2920 Charlottenlund, Denmark
3Biostatistisk Afdeling, Københavns Universitet, Øster Farimagsgade 5, Opgang B, Postboks 2099, 1014 Copenhagen, Denmark
4Oceanlab, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, UK

ABSTRACT: Baited cameras are often used for abundance estimation wherever alternative techniques are precluded, e.g. in abyssal systems and areas such as reefs. This method has thus far used models of the arrival process that are deterministic and, therefore, permit no estimate of precision. Furthermore, errors due to multiple counting of fish and missing those not seen by the camera have restricted the technique to using only the time of first arrival, leaving a lot of data redundant. Here, we reformulate the arrival process using a stochastic model, which allows the precision of abundance estimates to be quantified. Assuming a non-gregarious, cross-current-scavenging fish, we show that prediction of abundance from first arrival time is extremely uncertain. Using example data, we show that simple regression-based prediction from the initial (rising) slope of numbers at the bait gives good precision, accepting certain assumptions. The most precise abundance estimates were obtained by including the declining phase of the time series, using a simple model of departures, and taking account of scavengers beyond the camera’s view, using a hidden Markov model.

KEY WORDS: Deep sea · Coryphaenoides · Lander · Hidden Markov model · Population · Wildlife census

INTRODUCTION

Estimates of organism abundance are fundamental for marine ecology, but particularly difficult in many circumstances that preclude the intensive use of trawl sampling, or acoustic survey, e.g. abyssal systems and areas such as reefs, where trawls cannot run or would damage the sea floor unacceptably. Priede & Merrett (1998) recommended the deployment of autonomous lander platforms equipped with bait and camera systems as a relatively low-cost and low-impact alternative. In early work, Priede et al. (1990) successfully fitted an empirical curve to the time series of scavenger numbers present at a bait on the sea floor; this was later used to estimate (the assumed constant) staying time at bait (Henriques et al. 2002). Additionally, Priede & Merrett (1996) found an empirical relationship $\lambda \propto \tau_1^{-2}$, between the time to first fish arrival, $\tau_1$, and environmental fish density, $\lambda$, determined independently by trawling. Following these discoveries, interpretation of statistics other than first arrival time had not succeeded in predicting organism abundance (Priede & Merrett 1998), and thus has not been considered further.

More recent emphasis has been placed on using mechanistic models of the arrival process (Priede & Bagley 2000, Bailey & Priede 2002, Collins et al. 2002). These models make assumptions about foraging behaviour and the spatial distribution of scavengers, as well as the prevailing current, swimming speeds and odour plume development (linear extension and diffusive spread). The models fall into 2 main categories—those assuming actively searching foragers (usually fish) and those, following earlier work by Sainte-Marie & Hargrave (1987), assuming that scavengers passively wait for signs of food arriving on a spreading plume. In reality there is a continuum between these 2 extremes depending on the speed of searching relative to passive diffusion. For passive scavengers, a descrip-
tion of the plume is most important, but the crux of models with active scavengers is accurate representation of their search strategy in relation to the current (Bailey & Priede 2002). There is good evidence that swimming in an approximately orthogonal direction to the current is optimal (Dusenbery 1989, Vabo et al. 2004) and is commonly displayed by scavengers (Priede et al. 1991, Bailey & Priede 2002). Consequently, Bailey & Priede (2002) derived a deterministic model of arrival rate for cross-current scavengers and showed it was able to predict first arrival times, though they found this measure was relatively insensitive to abundance above about 100 ind. km$^{-2}$.

Biologists with time series data collected from baited camera deployments are still faced with the question of how to make the most effective and justifiable use of the data in estimating organism abundance. This is not by any means a simple question, as it depends on arrival and departure statistics, scavenger behaviour throughout the feeding cycle, and the limitations of the equipment used. The aim of the present work was to provide guidelines for estimating abundance from baited camera data, specifically for fish scavengers that actively search, rather than sit and wait, for odour plumes. We shall first build a conceptual model of the processes determining numbers of fish seen at the bait. Then we will assess 3 indirect measures of abundance using these counts, in order of increasing use of the data. Each measure will be demonstrated using example data taken from observations of Coryphaenoides armatus in the Nazaré Canyon, west of Portugal (King 2006). The important attributes of each method will be illustrated, showing its strengths and weaknesses; in particular, we shall show how the precision of the techniques increases as more information is used. The ecological time scale to which our analysis applies is that of the time series of camera observations in a single deployment.

**CONCEPTUAL MODEL**

The number of fish attending the bait results from a balance between arrivals and departures (Sainte-Marie & Hargrave 1987). The arrival rate depends on the number that are attracted to the bait, which is determined by the abundance of scavenger fish able to detect the plume, and the proportion of them that respond by swimming to the bait. We note here that the presence of competitors and predators near the bait can affect the bait’s attractiveness (see Lapointe & Saint-Marie 1992), but such effects are separate from the main estimation problem and we do not deal with them further. Hence, we assume that fish that can detect the bait will attend it. Even with this assumption, assessing counts at the bait is complicated by the fact that fish may arrive at the bait, circle it, perhaps exiting the camera view and may repeatedly return to the bait before finally leaving the area around the bait (bait zone) altogether (Collins et al. 1999). These behaviours potentially undermine efforts to estimate abundance (Yau et al. 2001), but a common response has been to average observed numbers of fish over several replications of bait deployment; for example, Priede et al. (1994) took the maximum mean number observed per block of 15 image frames as a best estimate of true numbers. We hope to improve on such heuristics. To facilitate reference to calculations, the symbols used and their ranges have been collated in Table 1.

Arrival rate is stochastically related to population density. Departure rate depends on the number of fish present at the bait and the fish behaviour (determining residence time), and the observable fraction depends on both movements local to the bait and the visual scope of the camera. These processes are brought together in the conceptual model (Fig. 1), in which $n(t)$ is the expected (mean) number of fish that have been attracted to the bait, but are not in the view of the camera and $m(t)$ is the expected number that are photographed. Thus, in our model, fish are attracted to the bait zone at a stochastic rate $\rho_a(t)$ and switch between this state and the ‘in camera’ state at rate $\zeta$, finally departing the bait zone at a stochastic rate of $\rho_d(t)$ (Fig. 1).

We make a simplifying assumption that the switching rate between in-camera and out-of-camera states is symmetrical (individual fish in the region are equally likely to become apparent as become obscure) and is therefore $\zeta[n(t) - m(t)]$. Conservation of numbers (fish are neither created nor destroyed here) ensures that after a time $T$:

$$n(T) + m(T) = \int_0^T \left[ \rho_a(\lambda, t) - \rho_d(t) \right] dt \quad (1)$$

and inspection of flow rates yields the following pair of differential equations:

$$\frac{dn(t)}{dt} = \rho_a(\lambda, t) + \zeta m(t) - (\rho_d(t) + \zeta)n(t) \quad (2)$$

$$\frac{dm(t)}{dt} = \zeta[n(t) - m(t)] \quad (3)$$

The resulting time series of numbers at the bait has the following general features: a delay phase before the first arrival, a growth phase during which the arrival rate exceeds the departure rate, and a decay phase in which departures exceed arrivals and, hence, a maximum in numbers when the arrival rate equals the departure rate (these features are shown in Bailey & Priede 2002, their Fig. 3). Superimposed on this gross pattern, the time series shows random rises and falls due to movements in and out of the field of view, as well as the stochasticity of arrival and departure processes. The above equations serve to explain the processes involved, but they are con-
Table 1. Symbols and their definitions, the quantities in the model, their dimensions, their range and the values used here

<table>
<thead>
<tr>
<th>Description</th>
<th>Units</th>
<th>Range</th>
<th>Typical</th>
</tr>
</thead>
<tbody>
<tr>
<td>( A(t) ) Area from which fish will reach the bait in time ( t )</td>
<td>m²</td>
<td>( \Lambda \geq 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \alpha(t) ) A constant gathering speed terms in the stochastic model</td>
<td>m² s⁻²</td>
<td>( \alpha &gt; 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( D ) Diffusion coefficient of fish</td>
<td>m² s⁻¹</td>
<td>( D &gt; 0 )</td>
<td>0.01 c</td>
</tr>
<tr>
<td>( J ) Flux of fish</td>
<td>fish m⁻¹ s⁻¹</td>
<td>( J &gt; 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \lambda ) Mean density of scavengers in the environment</td>
<td>fish m⁻³</td>
<td>( \lambda \geq 0 )</td>
<td>( 10^4 )</td>
</tr>
<tr>
<td>( \Lambda ) Constant in an empirical model of number of fish observed</td>
<td>fish s⁻⁹</td>
<td>( \Lambda \geq 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \gamma ) Shape parameter of the Weibull distribution ( a )</td>
<td>–</td>
<td>( \gamma &gt; 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \beta ) Scale parameter of the Weibull distribution ( b )</td>
<td>–</td>
<td>( \beta &gt; 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \phi ) Non-linear regression scaling constant</td>
<td>–</td>
<td>( \phi &gt; 0 )</td>
<td>( 1 &lt; \phi &lt; 3 )</td>
</tr>
<tr>
<td>( q ) Quintile of a statistical distribution</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>( m(t) ) Expected number of fish in fish camera view</td>
<td>fish</td>
<td>( m(t) \geq 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( n(t) ) Observed number of fish in camera view</td>
<td>fish</td>
<td>( n(t) \geq 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \eta(t) ) Hypothetically ‘observed’ number of hidden fish</td>
<td>fish</td>
<td>( \eta(t) \geq 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( N(t) ) Expected number of fish arrived after time ( t )</td>
<td>fish</td>
<td>( N(t) \geq 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \mu ) Expected rate of reorientation in foraging fish</td>
<td>s⁻¹</td>
<td>( \mu \geq 0 )</td>
<td>( 10^3 )</td>
</tr>
<tr>
<td>( \rho_f ) Rate of arrival of fish at the bait zone</td>
<td>s⁻¹</td>
<td>( \rho_f &gt; 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \lambda_f ) Rate of departure of fish at the bait zone</td>
<td>s⁻¹</td>
<td>( \lambda_f \geq 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \tau ) A finite time after deployment of the baited camera</td>
<td>s</td>
<td>( \tau \geq 0 )</td>
<td>( 10^2 )</td>
</tr>
<tr>
<td>( \tau^* ) Time when observed number of fish becomes maximum</td>
<td>s</td>
<td>( \tau^* \geq 0 )</td>
<td>( 10^3 )</td>
</tr>
<tr>
<td>( u ) Speed of the current</td>
<td>m s⁻¹</td>
<td>( u &gt; 0 )</td>
<td>0.05</td>
</tr>
<tr>
<td>( v ) Fish searching speed against the current (upstream)</td>
<td>m s⁻¹</td>
<td>( v &gt; 0 )</td>
<td>0.05</td>
</tr>
<tr>
<td>( w ) Fish searching speed perpendicular to the current</td>
<td>m s⁻¹</td>
<td>( w &gt; 0 )</td>
<td>0.05</td>
</tr>
<tr>
<td>( x(t) ) Total number of fish in the bait zone</td>
<td>fish</td>
<td>( x(t) &gt; 0 )</td>
<td>–</td>
</tr>
<tr>
<td>( \hat{e} ) Estimate of parameter controlling rate of change of ( \rho_f(t) )</td>
<td>fish s⁻²</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>( \zeta ) Switching rate in and out of camera view</td>
<td>s⁻¹</td>
<td>( \zeta \geq 0 )</td>
<td>–</td>
</tr>
</tbody>
</table>

aAs \( \beta \) increases, the PDF of the distribution lowers and spreads (see Johnson et al. 1994).
bAs \( \gamma \) increases, the PDF of the distribution becomes more symmetrical (Johnson et al. 1994).
cUnsupported by published data.

MODELS OF FISH ARRIVAL RATES

Two models will be considered: the first assumes that fish swim with constant velocity across the current (geometric model) and the second allows for random direction switching (diffusion model). The models give different predictions on how the number of arriving fish increases with time; empirical estimation of this rate will later be used to select the model which best fits a time series of fish arrivals.

Geometric model of fish arrivals.

We assume a constant velocity water current, with fish searching orthogonally (cross-current) for odour plumes. Given that fish searching speed is likely to be much greater than the odour diffusion rate (see Yen et al. 1998, Webster & Weisburg 2001), diffusive spreading has a negligible effect on arrival times. This greatly simplifies the problem by reducing the plume to a 1-dimensional target extending in space at the same rate (and in the same direction) as the current.

We use a coordinate system with the bait as the origin, with the positive \( y \)-direction defined by the current direction as it flows with constant speed \( u \). Fish move perpendicularly to the current (the \( x \)-axis) at a constant speed \( w \); on average, half of them move in the positive \( x \)-direction and the other half move in the negative \( x \)-direction. Once they encounter the plume, they swim up it at a speed \( v \) over the substrate by swimming faster than the opposing current. We also assume that fish act independently of one another, are equivalent in all respects, swim with constant velocity (except where stated) and that there is only 1 attractant (these fish cannot be distracted).
At time 0 the bait is placed at coordinates (0, 0). At time \( t \in [0, T] \), the bait can be detected in the set \( \{(x,y): x = 0, 0 \leq y \leq ut\} \)—this defines the plume as a line extending in the \( y \)-direction at a constant rate \( u \). Since fish can swim both left and right across the current, we assume half of them do each, and, since the system is symmetrical about the plume’s axis, we can simplify by considering only 1 side (halving the swept area), and assuming 1 swimming direction (doubling the fish interceptions), cancelling factors of 2, this is equivalent to the complete system. A fish starting at position \((x,y)\), \( x \geq 0, y \geq 0 \), swimming to the left (direction \(-x\)), can reach the plume at time \( x/w \) and the bait at time \( x/w + y/v \). Thus, for the fish to arrive at the bait, the following must be true: \( x/w + y/v \leq T \) or \( y \leq vT - vx/w \). Since the fish crosses the line \( x = 0 \) at time \( x/w \), it will only detect the bait plume if \( x/w \geq y/u \) or \( y \leq ux/w \). Therefore, between time 0 and time \( T \) the fish arriving at the bait must have been in the following triangular region at time 0:

\[
\{(x,y): x \geq 0, y \geq 0, y \leq vT - vx/w, y \leq ux/w\}
\]

which we call the ‘swept area’ \( A(T) \). Fig. 2 illustrates the geometry of this argument, and Fig. 3 shows how the 3 boundaries defining the swept area are used to calculate its size for a given value of \( T \):

\[
A(T) = \frac{1}{2} uvT^2 / (u+v) = \alpha T^2
\]

defining a constant \( \alpha \).

If the initial configuration of fish in the plane is a Poisson process with intensity \( \lambda \) (meaning a random 2-dimensional distribution of mean density \( \lambda \)), then the number of fish expected to have arrived at time \( t \) is Poisson distributed with an expected value (denoted by \( E[N_t] \)):

\[
E[N_t] = \lambda \alpha t^2
\]

Correspondingly, the time of arrival of each fish, marked on a time line, is a Poisson process of intensity:

\[
\frac{\lambda}{dt} \frac{dA}{dt}
\]

Assuming continuous linear growth of the plume, this intensity will grow linearly in time. Ultimately, the plume will be diluted below the detection threshold of searching fish, from this point the quadratic scaling would be replaced by a linear extrapolation giving a constant arrival rate. However, for simplicity we assume that at least until the first fish arrives, the plume is not truncated. Since Lokkeborg et al. (1995) found sablefish Anoplopoma fimbria to be able to detect food odour plumes over 1000s of metres and since dispersion is likely to be small over this scale (Zimmer-Faust et al. 1995), we expect the assumption to be reasonable over the time scale of several 10s of hours, which is typical of bait deployments.

**Diffusion model of fish arrivals.** Relaxing the assumption that fish swim with constant velocity forever, we allow them to occasionally turn in the opposite direction during cross-current foraging. We call this behaviour ‘reorientation’ and assume that it occurs at independently random times, thus constituting a Poisson process for the individual fish. We denote the expected rate of reorientation as \( \mu \) and assume it to be constant.

When the time since deployment of the bait is much shorter than \( 1/\mu \), we do not need to take reorientations into account, but, when it is much larger, the movement of the fish can be approximated with Brownian
motion (Okubo 1980), characterised by an equivalent diffusivity, $D = w^2u$ (since with orthogonal searching, this is effectively a 1-dimensional system).

In this diffusive model, we can estimate the flux of fish to the bait by first considering the diffusion problem

$$C = D \nabla^2 C$$

with the absorbing boundary $C(0, t) = 0$, far field $C(\infty, t) = C_\infty$ and initial condition $C(x, 0) = C_x$. In this partial differential equation system, used to describe the spread of particles (in our case fish) and define diffusion, the plume must reach distance $\lambda$ far field.

We find the probability density function (PDF) of $\tau_1$ by differentiating with respect to time:

$$P(\tau_1) = \gamma \alpha \lambda \tau_1^{-2} \exp(-\lambda \alpha \tau_1^2)$$

We recognise this density of $\tau_1$ to be that of a Weibull distribution (which is the subject of Chapter 21 in Johnson et al. 1994), with a shape parameter of $\gamma$ and scale parameter $\beta = 1/(\lambda \alpha)^{1/\gamma}$.

Note that in the geometric model described above, $A(t)$ is quadratic in time (assuming the plume does not truncate), so $\gamma = 2$, but using the more flexible diffusion model, the scaling is with $\sqrt{t}$, giving the value of $\gamma = \frac{3}{2}$ in Eq. (12).

We need to estimate the Weibull scale parameter $\beta$ as it provides the means for estimating $\lambda$ from $\tau_1$ via Eq. (12). Irrespective of the shape parameter (so for any model of arrivals founded on the assumption of a Poisson distribution of fish in the environment), the maximum-likelihood estimator for $\beta$ is $\hat{\beta} = \tau_1$ (Johnson et al. 1994, p. 656), so the variance of the estimator is equal to the variance of the first arrival time, which is known from the properties of the Weibull distribution:

$$V[\hat{\beta}] = V[\tau_1] = \beta^2 \Gamma(1 + \frac{2}{\gamma})$$

where $\Gamma(\alpha)$ is the Gamma function (a generalisation of the factorial).

We will now determine the precision of estimating fish abundance ($\lambda$) from first arrival times, irrespective of the precise model used for the arrival process.

Assuming $\alpha$ is known (i.e. the speeds of fish and current), we obtain an estimator for $\lambda$, using the definition of the scale parameter above:

$$\hat{\lambda} = \frac{1}{\alpha \beta^2}$$

In this, $\hat{\beta}$ is distributed as $\tau_1^{-1}$ which is an exponential distribution with mean $\beta$ (Johnson et al. 1994). $\alpha \hat{\lambda}$ must be distributed the same as $1/\beta^2$, which is the reciprocal of an exponential distribution, the mean of which is $\beta$. 

---

**Distribution of first arrival times.** First arrival times are the standard measure for estimating abundance using deterministic models (following Priede & Bagley 2000). Here, we derive the stochastic equivalent and, from this, determine the theoretical precision of abundance estimates based on first arrival time, assuming that the camera accurately records the true arrival time of the first fish. The following analysis applies for both the geometric and diffusion models, and more generally.
The exponential distribution is a special case of a Gamma distribution, having a shape parameter \( a = 1 \). A classic result is that if any variable \( X \) follows a Gamma distribution with any shape parameter \( a \), then its reciprocal \( Y = 1/X \) follows an inverse Gamma distribution with shape parameter \( a \). Unfortunately, it is also well known that the inverse Gamma distribution having shape parameter \( a = 1 \) has no finite expectation (implying that it cannot be predicted). Strictly, \( \mathbb{E}[Y] < \infty \) if \( a > 1 \), so our case is right at the limit of expectations existing. Because \( \mathbb{V}[Y] < \infty \), only if \( a > 2 \), the present problem is deep within the range having infinite variance, so no sample of \( \tau_i \) can yield an estimate \( \hat{\lambda} \) with non-zero certainty. In practice, the initial disturbing effect of the lander arriving on the bottom makes the assumption of Poisson arrivals invalid for a short time from the start, where an immediate visit from a fish is practically ruled out. This ‘smoothes’ the extreme conclusion of the statistical theory somewhat. Excluding the initial ‘disturbance transient’, the assumed Poisson distribution is readily justified as being the standard null model (minimum assumptions) for any random distribution in space. Thus, using well-known and long-established probability theory, we have shown that for a range of reasonable arrival models, assuming fish do not show social interactions and are not distracted from the bait, then the time of first arrival is a very poor predictor of their abundance.

**REGRESSION MODEL**

Using the rising phase of the time series. Next we examine a regression on the rising phase of the time series to estimate arrival rate and thereby abundance.

For practical purposes, we define the rising phase as the region from \( t = 0 \) to the time of arrival of the fish causing the maximum number to be observed together (which we label as \( \tau^* \)). The start of the time series is chosen because fish are potentially arriving from \( t = 0 \). The time when numbers reach maximum will not usually be the exact end of the rising phase, because the trend in expected numbers is superimposed with stochastic variation. However, since the distribution of the resulting error is approximately symmetric about the expected number-maximum, the observed maximum is close to an unbiased estimator.

The analysis assumes that observations are independent and that departure rate is zero during the rising phase (\( \hat{\rho} = 0 \) in \( t = 0, \tau^* \)) and that all fish attracted to the bait are seen; hence, arrivals are measured by \( m_t = m(t) \) (see Fig. 1; error of these assumptions will underestimate abundance).

Non-linear regression, describing the model \( m_t = \Lambda \phi t^\phi \), accommodates both the geometric cross-current forager (where \( \Lambda = \lambda \alpha \) and \( \phi = 2 \)) and the diffusion approximation (where \( \Lambda = \frac{\varphi}{\varphi + \alpha} \lambda \phi (D/\pi) \) and \( \phi = \frac{\varphi}{2} \)), but also permits a purely empirical estimate of \( \Lambda \) and \( \phi \), for which we have no theoretical explanation (it may involve complicating factors such as turbulence of the plume). This empirical fit should be included to demonstrate the plausibility (or otherwise) of the theoretically justifiable options. Thus, we have 3 regression models to compare (linear in the parameter in the first 2 cases and non-linear in the last case), summarised below.

<table>
<thead>
<tr>
<th>Model</th>
<th>Formula</th>
<th>Constraints</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1</td>
<td>( \mathbb{E}[m_t] = \Lambda \tau^2 )</td>
<td>linear geometry</td>
</tr>
<tr>
<td>Model 2</td>
<td>( \mathbb{E}[m_t] = \Lambda \phi t^\phi )</td>
<td>diffusion limit in fish behaviour</td>
</tr>
<tr>
<td>Model 3</td>
<td>( \mathbb{E}[m_t] = \Lambda t^\phi )</td>
<td>empirical model</td>
</tr>
</tbody>
</table>

**Regression predictions.** Here, we show the method in use on exemplary data taken from observations of *Coryphaenoides armatus* in the Nazaré Canyon, west of Portugal (King 2006). Normal regression assumes that errors are approximately normally distributed with zero mean and equal variances. Inspection of the residuals (using residual and normal quantile plots, Fig. 4) for the exemplary data does not support this assumption, especially as the variance can be seen increasing with fitted values.

Conversely, our theoretical models of arrival assume that \( m_t \) is Poisson distributed—chosen as it is a neutral model (zero information) for the spatial distribution of fish. To test this, we transformed the data prior to regression. Assuming that \( m_t \) follows a Poisson distribution with mean value \( \lambda t^\phi \), then \( \sqrt{\hat{m}_t} + \sqrt{\hat{m}_t + 1} \) will approximate a normal distribution (especially for small values of \( \lambda t^\phi \), as here), with an approximate mean value of \( 2\sqrt{\hat{\lambda} t^\phi} \) and unit variance (Freeman & Tukey 1950).

The normal quantile plots on transformed data (Fig. 5) provide statistical justification for these Poisson assumptions. Fitting the transformed models gave the results provided in Table 2.

The fitting of these models to the data is shown in Fig. 6, which indicates that both Models 2 and 3 have been very successful, the deviance values (Table 2) confirm this. It is impossible to distinguish Models 2 and 3 in the fitting of plots, because the empirical fit for \( \phi \) (Model 3) gave an estimate very close to \( \frac{3}{2} \), which

Table 2. Results from regression models, assuming \( \sqrt{\hat{m}_t} + \sqrt{\hat{m}_t + 1} \) normally distributed around twice the square root of the estimated mean. Deviance is the residual sum of squares

<table>
<thead>
<tr>
<th>Model</th>
<th>( \hat{\Lambda} )</th>
<th>SE(( \hat{\Lambda} ))</th>
<th>( \hat{\phi} )</th>
<th>SE(( \hat{\phi} ))</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1</td>
<td>0.10577</td>
<td>0.00272</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 2</td>
<td>0.28474</td>
<td>0.00613</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Model 3</td>
<td>0.29025</td>
<td>0.06177</td>
<td>1.4902</td>
<td>0.1084</td>
<td></td>
</tr>
</tbody>
</table>

This method is easy to implement: Models 1 and 2 are simply linear regressions. Model 3 is non-linear in the \( \phi \) parameter, adding a slight complication, but it is still simple to implement with standard statistical software.

**HIDDEN MARKOV MODEL**

Using the whole time series. The maximum use of information theoretically yields the highest achievable precision. In this section we will show how the whole time series can be analysed, using a model of departures from the bait of fish both seen and unseen by the camera.

Referring to Fig. 1, we regard \( n(t) \) as hidden and the \( \rho \) and \( \zeta \) terms as parameters that can be estimated using the statistical technique of a hidden Markov model (HMM) (Cappé et al. 2005)—now commonly used in automatic speech recognition. With this method, the system represented by Fig. 1 is assumed to be a 2-state Markov process \( (m_t, n_t) \), with parameters estimated from \( m_t \) (again, using the non-italic font to denote observed counts). The 'hidden state' is the number of fish at the bait, but outside the camera view \( (n_t) \).

We make the simplifying assumption that fish move among visible and hidden states between camera shots, so the observed \( m_t \) at each time step is a sample from a binomial distribution with number parameter \( x_t = n_t + m_t \) and some constant probability parameter \( p \). This \( p \) corresponds to the visible fraction of the fish at the bait.

Since the diffusive model of arrivals (Eq. 9) was the best supported by regression in the previous section, it is chosen to represent arrivals here, so we assume \( \rho_{\text{in}}(\lambda, t) = \rho_{\text{in}} / t \) (note tilde notation for empirically estimated parameters). We aim to estimate the prefactor \( \rho_{\text{in}} \) to derive from it a fish abundance estimate \( \hat{\lambda} \) using Eq. (9).

Now a model for departures is needed. The mean flux away from the bait zone at time \( t \) is proportional to the number of fish present at \( t \). To take account of the behaviour of fish towards a depleting bait, we define the departure rate \( \rho_{\text{out}} \) as follows: The probability of any fish leaving in a short time interval \( t \) to \( t + h \) is set to \( \rho_{\text{out}} h \) (approximated to first order in \( h \)), which we assume to be a linear function of time. However, we continue

---

**Fig. 4.** Diagnostic plots of models for untransformed data. (A) Model 1, (B) Model 2 and (C) Model 3. Left column: residuals against fitted values for the 3 models. Right column: quantile plots (empirical quantiles of residuals against quantiles of the standard normal distribution), reference lines pass through the first and third quartiles.
(This moment method is probably very close to a maximum-likelihood estimate, and reduces computational complexity significantly). We then tabulate the fit, i.e. the profile likelihood, for each combination of \( \hat{\gamma} \) and \( \hat{\rho} \). The parameter estimate is then chosen as that parameter combination which results in the largest profile likelihood, i.e. we tune the estimator to optimise predictions of the number of fish in view at the next image frame. Further details are given in Appendix 1.

**Predictions.** Fig. 7 shows the negative log-likelihood (often shortened to likelihood) of parameters \( \gamma \) and \( \rho_0 \). The optimal estimate, defining the minimum of this function, is at \( \hat{\gamma} = 0.0011 \) min\(^{-2} \) and \( \hat{\rho}_0 = 0.33 \). An approximate 95% confidence region is given by parameter values for which the likelihood does not exceed the minimum value by \( > 2q \), where \( q \) is the 95% quantile in a chi-squared distribution with the number of degrees of freedom equal to the number of estimated parameters. In the figure, this region is inside the \( I = 455 \) contour line.

Note that this predicts about one-third of the fish present in the bait zone are visible to the camera. The predicted value of \( \gamma \) in this case, means that a fish in the bait zone at peak numbers time \( t^* \) will stay for at least 34 further minutes with 50% probability (found from solving \( \exp[-\int_0^t \hat{\rho}_d(t)dt] = 0.5 \)). Fish that arrive later will tend to stay a shorter time, since the departure rate grows with time.

Fig. 8 shows the profile likelihood for the prefactor in fish arrival rate. We see that the maximum-likelihood estimate is \( 0.061 \) min\(^{-3/2} \), with a 95% confidence interval between 0.044 and 0.091. From this we can find the number of fish having arrived in the bait region at time \( t \): \( N_t = \int_0^t \rho_0 \gamma e^{-\rho_0 \gamma t} dt = 0.041t^{3/2} \) (in minutes). Using the estimate \( \hat{\rho}_0 \), this predicts that 0.013 fish \( \gamma \) fish will be visible to the camera (as long as they have not begun leaving, i.e. for \( t < t^* \)). This is close to half the prediction made by the regression method in the previous section (there, Model 2 gave 2.43 fish would be present), but that had assumed the visible fraction \( \rho = 1 \).

Using the parameter estimates gives a model of predicted numbers of fish in the bait zone \( (m_0 + n_0) \), the output if which is shown in Fig. 9, together with the observed number of fish. This result demonstrates the potential for the camera to underestimate numbers, a...
phenomenon now empirically confirmed by Jamieson et al. (2006) (though with a different lander to that used in generating the test data). Some may be surprised at the closeness with which the HMM model follows the data. The explanation is that the HMM is not a simple 3-parameter model (as often encountered in basic statistics), but a Markov model, which at each time step uses the whole time series along with the 3 parameters in a constantly updating calculation of expected numbers in the next photoframe. The fact that it follows the data consistently suggests that the parameter estimates are good.

**DISCUSSION**

Having examined 3 different methods for estimating abundance from fish counts at a bait, we are in a position to make recommendations for studies with cross-current foraging fish in reasonably stable currents. The first of these may be very surprising for biologists who have relied on first arrival times for their estimates. This measure was found to have a theoretically infinite variance and, in practice, to make a very poor estimator, as long as we can assume that fish do not socially interact, or become distracted from the bait. This finding is independent of the specific model of fish arrivals used, as it is a consequence of assuming a random distribution of fish in the environment. The weakness of first arrival time as a predictor had been obscured by the use of deterministic models, which did not allow uncertainty to be quantified. Despite several reports of correlations between $\tau_1$ and independently measured abundance (e.g. Sainte-Marie & Hargrave 1987), there is no support from statistical theory for using first arrival times.

Conversely, a regression on the rising phase of the time series (the period until maximum numbers are expected), assuming Poisson distribution of residuals and a diffusive scaling of arrival rate, gave a precise measure of abundance with the test data. This method is theoretically sound and simple to use, so we recommend it for circumstances where its assumptions are found to hold. These assumptions are specifically that fish behave independently, are distributed at random in the environment, and that all fish arriving at the bait are seen upon arrival. Further, that fish do not leave
the bait until after maximum numbers are observed, that the plume does not change greatly in direction during the rising phase, and that the usual assumptions for regression hold.

The more flexible method of HMM is recommended for its smaller set of assumptions, though it incurs a cost in complexity and additional parameters to be estimated. The assumptions of the HMM method are that fish are distributed randomly in the environment, act independently (including at the bait) and that the plume does not change greatly in direction during the time series (though the method could be adapted to cope with violations of the latter 2 assumptions). We wish to emphasise that it is very important to determine if the assumptions of any method are met prior to use.

In our example, for models of both the regression and HMM methods, we introduced a new parameter $D$, defined as fish searching diffusivity. Estimates of $D$ should be sought if this simple and flexible model is to be used. $D$ has the form of swimming speed squared, divided by the frequency of changing direction whilst searching for plumes: $D = w^2/\mu$. Search speeds ($w$) are often known, but new effort is needed to estimate turning frequencies ($\mu$) from observations of fish behaviour. Abundance estimates are sensitive to $D$, which is much less than their sensitivity to swimming speed, so, given a reasonable estimate of a fish’s turning frequency $\mu$, a working estimate of $D$ is attainable. It is possible to interpret $D$ more broadly as an empirical parameter that depends in part on non-linear extension of the plume, non-ideal swimming strategies of the fish and other factors that ‘spoil’ the theoretical ideals of the geometric model. However, a calibration based on independent abundance estimates (e.g. from trawls) would be necessary to estimate $D$, following this interpretation.

The regression and, in our example (though not necessarily or generally), the HMM method assumed that departure rate from the bait is zero until the maximum number of fish is seen ($\tau^*$). Strictly, this is not likely, partly because of randomness in fish behaviour and partly because the maximum should appear when the departure rate exceeds the arrival rate, which by definition is greater than zero. The resulting bias underestimates abundance in the regression method. It is therefore very important to ensure that this assumption is a reasonable approximation (i.e. that the maximum occurs at a time after deployment that is less than the expected staying time of a fish). The HMM method is less affected by this bias from the rising phase, because the iterative fitting can compensate using the remainder of the time series. If there is a long rising phase, we recommend the HMM method with some simple departure model designed to reflect the researchers’ beliefs about departures. In other words, the HMM method should be customised to the particular case for which it is to be used.

Practical application of the regression method is simple, using most statistical software packages. Time acts as the independent variable in a univariate non-linear regression for number of fish observed in each camera exposure (as in the described Model 2). The intercept should be set as zero (no fish at time zero), leaving the slope to be estimated, giving $\Lambda$ (as in Model 2), which enables $\lambda$ to be found from the various velocity estimates. We illustrated diagnostic plots to check that the assumptions of this method support its use; we especially recommend residual and quantile plots for this. Practical use of the HMM method requires some programming, for example, in a statistical or mathematics package—details are provided in the Appendix.

The problem caused by fish attracted to the apparatus, but not photographed on the bait (Collins et al. 1999) is well known and has been demonstrated by Jamieson et al. (2006, admittedly using a design of lander that is not usual for abundance estimation). The HMM method estimates the size of the resulting bias simultaneously while estimating arrival and departure rates. In the example shown, the HMM method estimated an arrival rate close to half that of the regression method when using the same model of arrivals over the same section of the time series. Independent measures of the ‘hidden fraction’ of fish would be hard to obtain, unless cameras were set to observe the lander system.

![Fig. 9. Examplary data (counted individuals in each photo) with hidden Markov model (HMM)-fitted estimates. HMM with full knowledge of observations (-----); model based on parameter estimates with the mean of observed count (.....); model of observed (visible) fish only, based on mean observed count (-----)].
The HMM method requires a model of departures as well as arrivals. Priede & Merrett (1998) fitted an empirical curve to the estimated staying time (which determines departure rate) using the time of maximum number of fish \( (t^*) \) minus the first arrival time \( (t_1) \), thus assuming staying time to be constant. However, bait depletion and scavenger competition mitigate against this assumption, especially for long time series. In principle, we could understand both effects in terms of optimal foraging theory, as suggested by Priede & Merrett (1998), who showed that staying time (as they defined it) declined with fish abundance (independently determined with trawls). However, using the marginal value theorem (Charnov 1976), suggested by this result, requires a model for competition and satiation, leading to considerable complications and introducing new parameters. For the present purpose, we suggest the parsimonious, single-parameter model in which the probability of departing in a small time interval increases at a constant rate with elapsed time. The gradual increase in departure probability that we hypothesise is most likely related to bait depletion, which can be estimated from the photographs. This could set limits (at least) on the \( z \) parameter of \( \rho_a \), so even crude estimates of bait depletion rate could be useful in using the HMM model. Clearly, there are opportunities to improve on this, but each development of sophistication needs to be justified by quantity and quality of data available.

Broadening the discussion, our overall model of fish behaviour can be extended in a number of ways to address specific biological issues. For example, species that show either gregarious or food-swarming behaviour could be represented by alternative statistical models of dispersion (the Poisson model being a null-hypothesis), and allowing for autocorrelation in the time series in the regression technique could probably accommodate most of these effects. Territoriality can be taken into account by truncating the arrival rate after a time representing territory size, and this approach can also be used to allow for rival attractants (e.g. natural food falls) in the environment. Changes in current velocity over measurement time are often observed in the deep sea and are almost inevitable (due to tides) in shallower seas. The result is a more complicated plume shape and perhaps changes in fish swimming velocities. To take account of this, our model could be treated as a piecewise fits to the number of observed fish, using different current parameters over different sections. More sophisticated modelling of the plume will allow a more precise description of how arrival rate depends on abundance, but not necessarily more precise abundance estimates, since additional parameters reduce statistical power. As stated earlier, it is possible to include plume spreading in the diffusivity parameter \( D \) of fish searching behaviour.

Acknowledgements. We thank D. M. Bailey for his very helpful suggestions and J. E. Beyer for facilitating the UK–Danish collaboration.

LITERATURE CITED

The hidden Markov model (HMM) method is implemented through an HMM filter. In the following, we briefly describe how this filter is constructed, so that those familiar with modelling can replicate the technique. In-depth treatments of the theory of HMMs are found in Cappé et al. (2005). The filter first aims to estimate the total number of fish, \( x_i \), in which \( x_i \) is a stochastic variable that may take integer values between 0 and a sufficiently large bound \( K \) on the total number of fish at the bait.

The filter needs the transition probabilities of \( x_i \) and consider \( x_{i+h} \), where \( h \) is a fixed short time interval. If a fish has arrived, then \( x_{i+h} = i + 1 \); the probability of this is \( g_{i+1}^h(t) = h \times \rho_d(t) \). If a fish has departed, then \( x_{i+h} = i - 1 \); the probability of this is \( g_{i-1}^h(t) = i \times h \times \rho_d(t) \). Alternatively, nothing has happened; the probability of this is \( g_i^h(t) = 1 - g_{i+1}^h(t) - g_{i-1}^h(t) \). These are valid approximations when \( h \) is small compared to \( \rho_d(t) \) and the rate of change of these functions. Typical camera sampling times of 30 to 120 s (in our example it was \( h = 90 \) s) will give sufficient resolution in most practical cases.

The predictive filter consists of \( \Phi(t) \), a (row) vector, the \( j \)th entry \( \Phi_j(t) \) of which is the probability that \( x_i = j \), given all observations strictly prior to \( t \). Similarly, the row vector \( \psi(t) \) has entries \( \psi_i(t) \) being the probability that \( x_i = i \), given all observations no later than \( t \). The ‘data update’ transforms \( \Phi(t) \) to \( \psi(t) \) by taking the observation \( m_t = m_i \), into account:

\[
\psi_i(t) = \frac{\Phi_i(t) P(m_t = m_i \mid x_t = i)}{\sum_j \frac{\Phi_j(t)}{P(m_t = m_i \mid x_t = j)}}
\]  

Here, \( \psi_i(0) = 0 \) and \( \psi_i(0) = 1 \) is a normalization ensuring that \( \sum_i \psi_i(t) = 1 \). These probabilities are computed using the assumption that, conditional on \( x_t = i, m_t \) is binomially distributed with number parameter \( i \) and probability parameter \( p \):

\[
P(m_t = m_i \mid x_t = i) = \binom{i}{m_i} p^m (1 - p)^{i-m_i}
\]  

The time update projects \( \psi(t) \) forward in time to obtain a prediction \( \Phi(t + h) \):

\[
\Phi_j(t + h) = \sum_{i=j-1}^{j+1} \psi_i(t) g_i^j(t)
\]  

The time update and the data update are iterated forwards in time; the initial condition is \( \psi_i(0) = 1 \) and \( \psi_i(0) = 0 \) for \( i \neq 0 \). At the end of the iteration, we evaluate the likelihood function \( L(\hat{x}, \beta) = \prod_{t=1}^{T} \psi_i(t) \). Recall that \( \beta \) is estimated by a moment method rather than with the likelihood method. The likelihood function is optimized numerically. For estimated parameters, we ‘smooth’ to obtain probability vectors \( \pi(t) \), with \( \pi_i(t) \) denoting the probability that \( x_t = i \), given all observations. This smoothing is an iteration backwards in time:

\[
\pi_i(t) = \psi_i(t) \sum_{j=1}^{i+1} g_j^i(t) \pi_j(t + h) \Phi_j(t + h)
\]  

with terminal condition \( \pi(T) = \psi(T) \).

### Appendix 1. Implementing the HMM technique
Influence of management practices and of scavenging seabirds on availability of fisheries discards to benthic scavengers

Robert W. Furness¹,*, Ann E. Edwards²,³, Daniel Oro⁴

¹Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK
²Alaska Fisheries Science Center—NOAA, REFM Division, 7600 Sand Point Way NE, Seattle, Washington 98115, USA
³School of Aquatic and Fisheries Sciences, University of Washington, Seattle, Washington 98195, USA
⁴Institut Mediterrani d’Estudis Avançats IMEDEA (CSIC-UIB), 07190 Esporles, Mallorca, Spain

ABSTRACT: There is great variation in discarding practice among fisheries in different parts of the world. Management systems result in some fisheries discarding mostly fish offal, much of which is macerated into small chunks, while other fisheries discard large (ca. 25 cm) whole fish. Scavenging seabirds consume high proportions of most categories of discarded fish and offal (typically 60 to 80% of discarded roundfish, 70 to 95% of discarded offal), but tend to avoid discarded benthic invertebrates and fish that are difficult to swallow, such as species with long spines or large flatfish. Amounts and composition of fishery discards and offal reaching benthic scavenging communities are clearly very strongly influenced by the intense but selective consumption by seabirds, and this alteration will depend strongly on details of the fishery management regulations and customs, such as whether or not waste is macerated. There is scope to adjust fisheries management practices to reduce the impact of offal and discards on scavenger communities.

KEY WORDS: Fisheries · Discards · Offal · Seabirds · Scavenger · North Sea · Mediterranean · Bering Sea

INTRODUCTION

It has been estimated that about 25 to 30 million tonnes (Mt) of fish were discarded by fisheries worldwide each year in the 1980s and early 1990s (Alverson et al. 1994), although some efforts have been made to reduce this amount in recent years (Hall & Mainprize 2005, Broadhurst et al. 2006). Since these discarded fish are predominantly dead or moribund, fishery discards, along with offal and lost bait, provide a large food supply to marine scavengers. This anthropogenic food supply may be much greater than the amounts of dead organisms naturally available in many marine ecosystems. Consumption of fishery waste by scavenging seabirds has been studied in a wide variety of areas where fishing practices differ considerably, such as the North Sea (Hudson & Furness 1988, Garthe et al. 1996, Catchpole et al. 2006), the Falklands (Thompson & Riddy 1995), South America (Bertellotti & Yorio 2000, González-Zevallos & Yorio 2006), the Mediterranean Sea (Oro & Ruiz 1997, Arcos & Oro 2002, Martínez-Abrain et al. 2002), the Baltic Sea (Garthe & Scherp 2003) and Australia (Svane 2005). In the present paper, we develop the ideas that taxon-selective and size-selective consumption of fishery discards and offal by scavenging seabirds, and management decisions by fisheries (for example, legal requirements to discard [or not to discard] at sea, setting of quotas, gear design and compliance, maceration of discards, mincing and submerging of offal, retention of waste for fishmeal and oil production, at-sea versus shoreside production) determine the amounts and composition of fishery waste sinking to the seabed. This may vary seasonally and geographically, as well as in relation to the abundance of alternate foods of scavenging seabirds (Garthe et al. 1996, Louza et al. 2006). Thus, it seems likely...
that seabirds can alter amounts of fishery waste reaching benthic scavenging communities, but the extent of this ‘filtering’ by seabirds has not been assessed in the context of food web structure and energy flows.

Seabirds are estimated to consume around 70 to 110 Mt of marine foods per year (Brooke 2004, Kar pouzi et al. 2007). Although most seabirds catch live prey, scavenging is a major feeding method employed by a small proportion of seabird species, especially by most of the albatrosses, some petrels and shearwaters, many gulls and skuas, and is a minor feeding method employed by some pelicans, gannets, boobies, frigatebirds and a few cormorants (Del Hoyo et al. 1992, 1996). Scavenging seabirds tend to be large species with energetically inexpensive locomotion (often using gliding or soaring flight), which can travel over long distances in search of food at sea and can feed on occasionally located large prey items. On a global scale, scavenging by albatrosses may represent the largest quantity of fishery waste taken by seabirds, though most studies of scavenging seabird ecology have focused on gulls and skuas.

Many scavenging seabirds have increased dramatically in numbers, and these increases have often been attributed to the feeding opportunities presented over many decades by fishery waste (Mitchell et al. 2004, Oro et al. 2004). However, fisheries may also kill scavenging seabirds through drowning on longline hooks and collision with fishing gear (González-Zevallos & Yorio 2006, Sullivan et al. 2006), while reduction in discarding rates by fisheries or certain changes in fishery management or practice can result in prey-switching by scavenging seabirds to kill smaller seabirds and their chicks (Votier et al. 2004). Better understanding of seabird foraging ecology and seabird–fisheries interactions may aid conservation and ecosystem management, including improvement of our understanding of the inputs of food from fisheries to benthic scavenging communities. This paper assesses the extent to which selective scavenging by seabirds may affect the inputs of fishery waste to benthic communities, and how these inputs are likely to vary as a consequence of differences in fishery management regulations and practice. We explore these issues by comparing and contrasting fisheries and associated scavenging seabirds, with a particular focus on 3 specific areas, the North Sea, the eastern Bering Sea and Aleutian Islands (BSAI), and the western Mediterranean Sea.

**MATERIALS AND METHODS**

We reviewed the literature on scavenging seabirds to extract information on the proportions of discards eaten by seabirds and how these proportions vary by discard type, size, fishery behaviour and statutory regulations affecting fishing and at-sea fish processing procedures. Combining these data with information on discarding rates in different fisheries, we compare the patterns in different regions and fisheries and outline general features of scavenging by seabirds that are consistent across this variation in fishery practice. We then use these data to assess for the first time the extent to which scavenging seabirds modify the amounts of fisheries waste that sink towards the seabed to provide foraging opportunities for pelagic and benthic scavengers. These calculations focus primarily on North Sea and Mediterranean seabird communities, where the most detailed studies of consumption of fishery waste by scavenging seabirds have been carried out, but, where possible, we have included comparable data from other parts of the world.

We computed a ‘seabird scavenging index’ as the mean numbers of a particular species following fishing vessels divided by the mean density of that species derived from ‘at-sea’ surveys. Thus, the ‘seabird scavenging index’ gives a relative measure of the extent to which particular species are attracted to fishing vessels rather than to natural food at sea. We also computed a ‘discard consumption success index’ as the number of discards swallowed by a particular seabird species during experimental discarding studies in relation to the numbers of that species following the fishing vessels. That index provides a measure of the relative success of different seabird species in obtaining discards from a particular fishery under prevailing conditions. We also combined data on the mean lengths of discards taken by different seabirds with the mean body masses of those species, to explore the size selection by seabirds as a function of their body sizes.

Calculations of offal and discards for at-sea processors in the BSAI fishery management region were derived from NOAA landings and products data for the Alaskan groundfish fishery.

**RESULTS**

**The North Sea**

In the North Sea, discards from trawl fisheries (i.e. demersal species of fish) have become a key food for scavenging seabirds (Garthe et al. 1996). Without fisheries, demersal species, such as haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus*, would not be available for these birds as they live too deep for scavenging seabirds to reach. The gadoid trawl fishery in the northern North Sea discards predominantly whole and rather large haddock and whiting, of around 20 to 30 cm in length, with rather few
flatfish and very few benthic invertebrates (Hudson & Furness 1988, Votier et al. 2004). Discards from the Norway lobster *Nephrops norvegicus* fishery consist of smaller roundfish, especially juvenile whiting of 10 to 15 cm, larger numbers of small flatfish, and large quantities of benthic invertebrates (Garthe et al. 1996, Catchpole et al. 2006). Discards from the beam trawl fishery in the southern North Sea tend to contain large quantities of flatfish and invertebrates with few roundfish (Garthe et al. 1996). All these fisheries discard whole fish, which are predominantly dead or moribund and which sink slowly and, hence, can remain close to the surface for some time owing to the turbulence caused by fishing vessel propellers. The most extensive study of discard consumption by North Sea seabirds (Garthe et al. 1996) showed higher consumption rates in winter than in summer, and that when discarding is performed continuously as a trickle during catch sorting and processing (as was then the normal procedure of fishermen on the observed vessels), seabirds consume very high proportions of offal (94 to 100%) and roundfish discards (70 to 92%), but only small proportions of discarded flatfish (10 to 35%) or benthic invertebrates (3 to 17%) (Table 1). Other studies in the North Sea have provided very similar results to this (Table 2). These data indicate that seabirds greatly modify the amounts of fishery waste sinking down towards the seabed (Fig. 1).

Table 1. Percentages and sample sizes of discarded offal, roundfish, flatfish and benthic invertebrates eaten by scavenging seabirds at different times of year in the North Sea (data from Garthe et al. 1996). Invert.: invertebrates

<table>
<thead>
<tr>
<th>Season</th>
<th>Offal (%)</th>
<th>Roundfish (%)</th>
<th>Flatfish (%)</th>
<th>Benthic invert. (%)</th>
<th>Sample size (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>100</td>
<td>92</td>
<td>35</td>
<td>17</td>
<td>6020</td>
</tr>
<tr>
<td>Spring</td>
<td>94</td>
<td>76</td>
<td>22</td>
<td>8</td>
<td>10344</td>
</tr>
<tr>
<td>Summer</td>
<td>94</td>
<td>70</td>
<td>10</td>
<td>3</td>
<td>8518</td>
</tr>
<tr>
<td>Autumn</td>
<td>97</td>
<td>82</td>
<td>20</td>
<td>3</td>
<td>5928</td>
</tr>
<tr>
<td>Sample size</td>
<td>5715</td>
<td>21848</td>
<td>2345</td>
<td>902</td>
<td>30810</td>
</tr>
</tbody>
</table>

Table 2. Average consumption rates (% swallowed) by scavenging seabirds determined by experimental discarding from commercial fishing vessels during routine processing of catches (including discarding by the fishermen) in different regions and fisheries, and related to the typical size (length in cm) of fish experimentally discarded in the study fishery

<table>
<thead>
<tr>
<th>Region</th>
<th>Offal Rate (%)</th>
<th>Roundfish Rate (%)</th>
<th>Flatfish Rate (%)</th>
<th>Invertebrates Rate (%)</th>
<th>Source of data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southern North Sea (whitefish trawl)</td>
<td>96</td>
<td>90</td>
<td>22</td>
<td>22</td>
<td>15</td>
</tr>
<tr>
<td>North Sea (<em>Nephrops</em> trawl)</td>
<td>–</td>
<td>80</td>
<td>–</td>
<td>18</td>
<td>–</td>
</tr>
<tr>
<td>Baltic Sea</td>
<td>87</td>
<td>81</td>
<td>20</td>
<td>8</td>
<td>18</td>
</tr>
<tr>
<td>Western Mediterranean Sea</td>
<td>–</td>
<td>54–78</td>
<td>10</td>
<td>52–70</td>
<td>8</td>
</tr>
</tbody>
</table>
North Sea in summer, northern fulmars *Fulmarus glacialis* and great black-backed gulls *Larus marinus* were the most numerous seabirds at trawlers, but the highest scavenging index scores were seen for great black-backed gulls and great skuas *Stercorarius skua* (Table 3). Fulmars and lesser black-backed gulls *Larus fuscus* also showed high aggregation at vessels, and lower index scores resulted for herring gulls *Larus argentatus* and northern gannets *Morus bassanus*. Most offal was consumed by northern fulmars, and a high proportion of discarded roundfish was taken by great black-backed gulls (Table 3). Smaller proportions were taken by gannets, great skuas and herring gulls (Table 3). Despite their numerical predominance at fishing vessels, northern fulmars swallowed rather few discards, and so had a discard consumption success index of only 0.2, far lower than achieved by herring gulls (3.6), lesser black-backed gulls (5.3), great black-backed gulls (11.8), great skuas (28.9), or northern gannets (50.2). Fulmars primarily swallowed whiting <20 cm length and hardly took any whiting >25 cm, showing very strong selection for smaller fish than those typically being discarded by the trawl fishery in the north-western North Sea (Fig. 2). Comparison of the sizes of fish swallowed by seabirds of different sizes (Fig. 3) suggests that most of the variation in size preferences relate to differences in body size and so the ability of birds to swallow the fish easily. However, the species falling furthest below the regression line in Fig. 3 is the northern fulmar. This species seems to take relatively smaller discards than would be predicted from its body size.

North Sea fisheries show little seasonal variation in discarding rates, although amounts discarded vary among years according to recruitment strength of key fish species, such as whiting and haddock (ICES Work-
ing Group reports at www.ices.dk). Higher consumption rates by seabirds in winter (Table 1) may reflect increased numbers of gulls in the North Sea as a result of migrations of populations breeding at higher latitudes, but also probably reflect the fact that sandeels Ammodytes spp., a major food of most seabirds in the North Sea in summer, are in the seabed and unavailable to most seabirds in winter, so that there seems to be more competition for discards in winter in this region.

**The western Mediterranean Sea**

Although purse-seine fisheries also discard amounts of small pelagics due to fluctuations in market prices or to partly damaged catch, most discards come from trawl fisheries, and these have been the focus of study. Discarding rates in Mediterranean trawl fisheries can be high: ca. 45% in the north-eastern region (Aegean and Ionian Seas), and slightly lower, due to higher net mesh size, in the western areas (Gulf of Lyon, Catalan-Balearic Sea) (Machias et al. 2001, Mallol 2005). Furthermore, discarding rates are very variable, ranging from 8 to 73% depending on year, season, area and targeted fish (Oro & Ruiz 1997, Arcos 2001, Martínez-Abrain et al. 2002, Mallol 2005). The number of species discarded can also be very variable (Sanchez et al. 2004). Studies of discard consumption by seabirds in the western Mediterranean Sea have found seasonal and regional variations, with higher consumption outside of the breeding season and in areas where Audouin’s gulls Larus audouinii are numerous; at the Ebro Delta 72 to 81% of discards were taken by seabirds; off Barcelona, 84%; at Mallorca, 64%; but at Benidorm, only 54% (Oro & Ruiz 1997, Arcos 2001, Martínez-Abrain et al. 2002). The sizes of discards from the Mediterranean trawl fishery were much smaller than those in the North Sea fisheries, with an average length of only around 10 cm for roundfish and 8 cm for flatfish (Table 2). Scavenging is also favoured by the discard of sardine Sardina pilchardus, which forms a large proportion of the catches (in several regions it is the predominant species by biomass in the catches). Discarding of sardines occurs when there is a fall in market interest in this species (Mallol 2005). Sardines are the main natural prey for most seabirds in the Mediterranean, so their discarding is very suitable for scavenging species, with consumption rates of up to 100% (Oro & Ruiz 1997, Martínez-Abrain et al. 2002).

Management of Spanish Mediterranean trawl fisheries involves periodical closures of the fishery (mora- toria) to protect stocks from over-exploitation, contributing, in turn, to sustainable management. Around the Ebro Delta, which is one of the most important fishing grounds for trawling in the Mediterranean, a trawling moratorium has been imposed for 2 mo each year since 1991, and, during these periods, the availability of discards to scavengers abruptly falls to zero. The area covers ca. 250 km of coastline and holds 11 harbours. Commercial catches from 1990 to 2005 were, on average, $30.0 \times 10^6$ kg yr$^{-1}$ (SE = $5.0 \times 10^5$); the main targeted species were European hake Merluccius mer- lucius and blue whiting Micromesistius poutassou. Several studies quantified fish discarded by trawl fisheries and discards consumed by scavenging seabirds (e.g. Arcos 2001). Similar studies were carried out at other areas (Oro & Ruiz 1997, Arcos & Oro 2002, Martínez-Abrain et al. 2002), and also used data from Mallorca (Balearic archipelago) for comparison: here oceanographic features are very different, with narrow continental shelves and lower productivity, resulting in much lower commercial catches ($1.4 \times 10^6$ kg yr$^{-1}$), different targeted species (mainly mullets Mullus spp., European hake, and red shrimp Aristaeus antennatus) and a smaller seabird community, with potential consequences on the amounts of discarded fish available for benthic scavengers.

A simple model was based on an equation estimating the discards (kg mo$^{-1}$) consumed by seabirds from the total commercial catches (DC, %)—while (1 – DC) is the percentage of discards sunk from the total commercial catches and available for benthic scavengers—to have a rough estimate of this parameter in a given time and area. We obtained DC by multiplying a set of variables, for which good quality data exist (see Arcos 2001; Table 2 present paper):

$$DC = CC \times DR \times CR$$

where CC was commercial catches (landings of the trawling fisheries), DR was discard ratio (relative to
landings) and CR was consumption rate (proportion of discards taken by seabirds). The model was applied during the breeding season of seabirds (from April to July) to the areas of the Ebro Delta and Mallorca Is. For each variable, we generated (by bootstrapping) a simulated data set, randomly drawn from the corresponding distribution. The resulting mean values were introduced in the previous equations to compute an averaged value of DC, and the process was run 1000 times, thus obtaining a probability distribution of DC means (J. Arcos et al. unpubl. data). The ratio of discards consumed by seabirds relative to landings (DR) was estimated at 0.371 (95% CI: 0.351/0.390) and 0.139 (95% CI: 0.131/0.147) at the Ebro Delta and Mallorca, respectively. The variability in the parameter DC in the Mediterranean is very high due to the high biodiversity in fish communities and the variability in targeted species, as well as the heterogeneity in seabird colony distributions, with decreasing fleets and breeding numbers from western to eastern parts of the sea. Even at small spatial scales, such as the neighbouring areas of the Ebro Delta, Barcelona and Mallorca, the variation is high depending on the type of haul, sea depth and type of substrate (see Table 4). Despite this variability, the amounts of discards sinking and available for benthic scavengers should be high despite the fraction consumed at the surface or just beneath by scavenging seabirds.

The eastern Bering Sea

The Bering Sea is characterized by concentrations of planktivorous, piscivorous and omnivorous birds, whose distributions are determined by ocean depths, currents and topographic features that determine prey distributions (Piatt & Springer 2003). Commercial fishing makes a considerable amount of food available to surface scavengers, possibly altering the distributions of some bird species. However, there is variation among fisheries in the BSAI fishery management region in the quantities, sources and seasonality of biomass returned to the sea and thus made available to seabirds and subsequently to benthic scavengers.

The midwater trawl fishery, which targets pollock Theragra chalcogramma is both one of the biggest and one of the most selective fisheries in the world, taking a catch of pollock valued at more than a billion US dollars per year. In the BSAI fishery management area in 2005, of the 805 652 t of fish brought on board at-sea processing vessels by the midwater trawl fishery, only 0.6% of the total catch was discarded back to the sea (Table 5). Another 0.8% of the total catch consisted of whole fish that might have been discarded back to the sea, but instead were made into fishmeal while at sea (Table 5). Thus, the high volume midwater trawl fishery provides few discards to seabirds or the marine ecosystem as a whole. In contrast, offal (the parts of the fish remaining after the marketable parts have been extracted) is produced and returned to the marine environment in prodigious quantities (see below). The bottom trawl fishery in the BSAI is smaller and much less selective than the midwater trawl fishery. Of >316 000 t of fish caught in the BSAI bottom trawl fishery, 22% were discarded back to the sea (Table 5). The longline fishery handles even smaller quantities of fish (ca. 145 000 t total catch), but is intermediate in its selectivity, returning 11% of the total catch to the sea. Because of differences in selectivity, the smaller bottom trawl fishery returns a greater biomass of discards to the ocean than does the large midwater trawl fishery (>69 000 t versus <5000 t).

The fisheries also vary in the quantity of offal returned to the marine environment. In 2005, at-sea processors for the midwater trawl fishery returned about 419 000 t to the sea, while at-sea processors for the bottom trawl fishery and the longline fishery returned about 53 000 and 56 000 t, respectively. These differences arise because the fisheries differ in the mean proportion of each fish that becomes offal, ranging from 53% in the midwater trawl fishery, which usually removes heads, guts, skin and bone, to 24% in the bottom trawl fishery, which may only head and gut fish, or simply sell them whole or merely bled (Table 5).

Table 4. Landed catches, discards and offal per haul (in kg), according to the type of haul and the area in the north-western Mediterranean. The ratio of discards versus landed captures is also provided (DR), as well as the percentage of discards a priori consumable by seabirds (consumable fraction, CF). Hauls: number of hauls. Data from Arcos (2001)

<table>
<thead>
<tr>
<th></th>
<th>Continental shelf</th>
<th></th>
<th>Upper slope</th>
<th></th>
<th>Mid-slope</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hauls</td>
<td></td>
<td>Hauls</td>
<td></td>
<td>Hauls</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Catches (kg)</td>
<td>23</td>
<td>124.2</td>
<td>13–550</td>
<td>36</td>
<td>184.4</td>
<td>57–850</td>
</tr>
<tr>
<td>Discards (kg)</td>
<td>31</td>
<td>174.8</td>
<td>20–1125</td>
<td>36</td>
<td>89.3</td>
<td>16–425</td>
</tr>
<tr>
<td>Offal (kg)</td>
<td>30</td>
<td>0.27</td>
<td>0–2</td>
<td>36</td>
<td>0.17</td>
<td>0–2</td>
</tr>
<tr>
<td>DR</td>
<td>23</td>
<td>176.8</td>
<td>47.2–730</td>
<td>36</td>
<td>56.1</td>
<td>8.2–212.5</td>
</tr>
<tr>
<td>CF</td>
<td>1</td>
<td>75.3</td>
<td>–</td>
<td>24</td>
<td>64.0</td>
<td>12.7–99.9</td>
</tr>
</tbody>
</table>
as well as in the overall quantity of fish processed. The presence of fishmeal and fish oil plants on board the larger processor vessels and the extraction of other secondary products, such as roe or meat from the cheeks, bellies, etc., reduces even further the amount of biomass returned to the sea (Table 5).

At-sea processors in the Bering Sea and Aleutian Islands are required by statute (Environmental Protection Agency regulations) to macerate all offal and virtually all discards discharged to the sea to chunks of approximately 1 cm in diameter. This has a considerable effect on the physical characteristics and, potentially, the fine-scale distribution of food presented to scavengers. These changes may potentially alter both the relative costs and benefits of boat-following for individual scavengers, as well as the competitive interactions within and between bird species, specifically increasing the benefit to smaller seabirds, such as fulmars, kittiwakes and shearwaters. No data currently exist quantifying the feeding patterns of seabirds behind fishing vessels in the Bering Sea (Table 5).

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offal (Table 5), also predominantly in a macerated form, and waste is predominantly produced in early spring and late summer/early autumn (Fig. 4). The trawl fishery in the western Mediterranean generates large quantities of discards comprising whole small fish, but little offal from fish gutted at sea (Table 4), but with short periods when the fishery is closed and no discarding occurs. In the North Sea trawl fisheries there is little seasonal variation, but large quantities of offal and large whole fish are discarded (Garthe et al. 1996; Table 2 present paper). Maceration of offal and discards by catcher-processors in the eastern Bering Sea make material more suitable for consumption by smaller scavenging seabirds and perhaps less attractive for larger scavenging seabirds, whereas, in the North Sea, the large size of most discards makes these unsuitable for smaller scavenging seabirds. Fishery closures and seasonal fisheries may result in scavenging seabirds being unable to rely on fishery waste as a consistent food supply, and this may lead to lower exploitation of this food resource by seabirds.

Selection by seabirds

Consumption rates were not significantly different for roundfish and flatfish discards in the Mediterranean studies, in contrast to the pattern seen in the North Sea, where seabirds tended to avoid flatfish. In the western Mediterranean, some discarded fish species were positively selected (e.g. sardine, bogue Boops boops, gadiforms), whereas others were avoided (e.g. chondrychthyes, gobids and dragonets) (Oro & Ruiz 1997, Arcos 2001). Most scavenging seabird species in the Mediterranean are surface feeders (terns and gulls) and exploit species remaining near or at the surface for some time (e.g. bogue and some gadiforms), while shearwaters can dive and probably catch fish that sink more quickly (e.g. anchovy Engraulis encrasicholus). The species most strongly avoided by seabirds in the Mediterranean tend to be roundfish with large spines that are obviously difficult for birds to swallow. In the North Sea, most roundfish discards are not spiny, and seabirds appear to avoid flatfish. The flatfish discarded by the North Sea fisheries tend to be rather large (typically 23 cm in the whitefish trawl fishery) and so will be difficult for seabirds to swallow. In contrast, flatfish discarded in the western Mediterranean tend to be much smaller (typically 8 cm), and this seems to be small enough that seabirds can more easily swallow these than spiny roundfish. This difference results in the contrasting pattern of discard selection demonstrated in Fig. 1. Essentially, seabirds select discards that are relatively easy to swallow, which is strongly influenced by seabird size and by fish morphology, as well as size. In all regions seabirds are likely to show less interest in discarded benthic invertebrates, while offal tends to be consumed quickly.

Implications for scavenging seabirds

In the North Sea, breeding numbers of scavenging seabirds have increased several fold during the 20th century, possibly due to improved body condition and breeding performance, resulting from the availability of this extra food (Mitchell et al. 2004). However, in recent years there have been large reductions in the amounts of demersal fish made available to scavenging seabirds in the northern North Sea, partly as a result of reduced fishing effort on gadoids and partly due to changes in technical measures, such as net mesh size and design (Votier et al. 2004, Hall & Main-prize 2005). In the western Mediterranean, there are also indications that discards support elevated breeding numbers of scavenging seabirds, although fishery moratoria may cause breeding failures and prey-switching interactions among seabird species (Arcos & Oro 2002, Oro et al. 2004). There is little information on the extent to which fishery waste in the eastern Bering Sea affects seabird numbers or distribution, although it is known that large numbers of northern fulmars and other seabirds scavenge on fishery waste. The practice of macerating waste to small bite-sized pieces (~1 cm) before discharge could have a considerable effect on its use by seabirds. Thus, it would be interesting to investigate consumption rates of offal and discards in the eastern Bering Sea. Evidence from studies in the North Sea suggests that maceration increases the suitability of waste for consumption by northern fulmars. It may be necessary to reduce waste to an essentially liquid form to make it unsuitable as food for seabirds.

Implications for benthic scavengers

In a wide variety of marine ecosystems around the world, scavenging seabirds consume a high proportion of discards from fishing vessels, and show strong selection for more easily swallowed items and probably for fish of higher calorific content. Some sinking discards that are not consumed by seabirds are probably eaten by pelagic fish, although there are few data on this. Some studies in the eastern Bering Sea suggest that Pacific cod may scavenge on sinking fishery waste, based on analysis of Pacific cod stomach contents that could be identified as macerated discards (Alaska Fisheries Science Center unpubl. data). The fisheries-derived biomass that reaches the benthic scavenging community will vary in quantity and species composi-
tion relative to that discarded at the ocean’s surface. The effect of seabird scavengers on marine ecosystems can vary seasonally, for example, in the North Sea seabirds take more discards in winter. Given the high rates of consumption by seabirds of offal and discarded fish, in at least some parts of the world, it would be inappropriate to infer that discarding always provides a means of recycling material back into marine fish via the benthos. Part of the nutrients taken up by seabirds from discards and offal will be excreted on land if these birds are roosting ashore or attending colonies, while the nutrients excreted at sea are likely to enter the pelagic ecosystem rather than the benthic.

Implications for future fisheries management

Our 3 examples, the North Sea, the western Mediterranean Sea and the eastern Bering Sea, provide highly divergent pictures of fisheries management practices, but common principles of discard use by scavenging seabirds. As a broad generalisation, scavenging seabirds take a high proportion of fisheries offal and discards, but avoid items of low nutritional quality (low energy content or low digestibility), such as benthic invertebrates, and avoid fish that are difficult to swallow, either due to large size, to shape, or to presence of spines and other defence structures. It is clear that management practices such as macerating discards greatly influence the suitability of this waste as food for seabirds and will alter the competitive balance between larger and smaller species. Seasonal closures of fisheries have a great impact on scavenging seabirds, by creating bottlenecks that may limit the numbers or breeding success of scavenging seabirds when they are forced to switch to more natural feeding. The highly selective consumption of fisheries discards and offal by seabirds will have a filtering effect moderating the amounts and types of waste reaching the benthic scavenging community. The current trend to reduce discarding is already having impacts on scavenging seabirds (Oro et al. 2004, Votier et al. 2004). However, we recommend that strong efforts should be made to reduce discarding as much as possible. We should not recommend a continuation of current discarding practices for the sake of scavenging seabirds, as these artificially sustain elevated populations of scavengers, and it would be preferable to see these populations brought back to pre-discarding sustainable levels. In particular, we should be aware of the problem of long-line bycatch of scavenging seabirds, which could probably be reduced if fishing vessels did not provide any offal or discards to attract these birds to feed at vessels. A policy of no discarding at sea, or of liquidisation of discards and offal before discharge, so that these no longer provide food for seabirds may be a significant mitigation measure to reduce the problem of longline bycatch of seabirds (Melvin et al. 2006) and the disruption to seabird communities caused by sudden changes in discarding practice (Votier et al. 2004).

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Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure

Euan S. Harvey1,4,*, Mike Cappo2, James J. Butler1, Norm Hall3, Gary A. Kendrick1,4

1School of Plant Biology (Botany M090), University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia
2Australian Institute of Marine Science, PMB 3, Townsville MC, Queensland 4810, Australia
3Centre for Fish and Fisheries Research, School of Biological Sciences and Biotechnology, Murdoch University, Murdoch, Western Australia 6150, Australia
4CRC for Coastal Zone, Estuary and Waterway Management, School of Plant Biology (Botany M090), University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia

ABSTRACT: Discriminating marine fish assemblages at broad scales can be difficult because of heterogeneity within their habitats, variability in patterns of behaviour and abundance of fish between habitats, and sampling biases in extractive fishing techniques when used across a range of habitats. Remote underwater video stations have recently been developed to help overcome these problems, but the use of bait as an attractant raises questions about bias towards scavengers and predators in samples of fish communities. We compared the ability of baited and unbaited underwater video stations to discriminate between fish assemblages inhabiting distinct benthic habitats in temperate and tropical continental shelf waters in Australia, to help test whether the bait attracted predatory and scavenging species to the video in disproportionate numbers in comparison to other trophic groups, such as herbivores. Data from baited video cameras displayed a clearer discrimination in constrained canonical analysis of principal coordinates of fish assemblages between marine habitats in both tropical and temperate environments. Analysis of the key trophic groups indicated that bait attracted greater numbers of predatory and scavenging species without decreasing the abundances of herbivorous or omnivorous fishes. There was greater similarity between replicate samples from baited video within habitats, implying that the use of bait will provide better statistical power to detect spatial and temporal changes in the structure of fish assemblages and the relative abundances of individual species within them.

KEY WORDS: Demersal fish assemblages · Underwater video stations · Bait · Remote sampling

INTRODUCTION

In topographically complex habitats, the relative abundance and distribution of individual species of fish is difficult to assess comprehensively. This is due to the heterogeneity of their habitats, variability in patterns of fish behaviour and abundance, and sampling bias in the techniques available. Numerous comparative studies have documented bias and selectivity among sampling methods (e.g. Willis et al. 2000, Watson et al. 2005). The coefficients of variation for some extractive techniques, such as fish trapping, can be so high that the power to detect large changes in sample means is weak, requiring levels of replication that would be unacceptable in areas such as marine parks (Williams et al. 1997, Cappo et al. 2003).

Underwater visual surveys by SCUBA divers in shallow waters, and by observers from submersibles in deeper waters, have enabled density estimates to be made for a variety of species in a range of habitats (e.g. Samoilys & Carlos 2000, Yoklavich et al. 2000). However, these surveys can be seriously biased for some
‘shy’ or cryptic species (Watson et al. 1995, Kulbicki 1998, Willis & Babcock 2000, Stewart & Beukers 2000, Watson et al. 2005). Other important drawbacks of these methods are the depth limitations of diver surveys and the prohibitive costs and limited availability of submersibles.

More recently, remotely operated video stations have been used to minimise the biases introduced by the presence of SCUBA divers (Willis & Babcock 2000, Willis et al. 2000, Westera et al. 2003) and those biases associated with gear selectivity inherent in baited trapping and hook-and-line surveys (Ellis & DeMartini 1995, Cappo et al. 2004). These studies followed the development of protocols to count and measure scavengers in abyssal depths using time-lapse still cameras or video cameras (Priede et al. 1990, 1994, Priede & Merrett 1996). Video-based techniques are now proving particularly useful in assessing the effects of marine protected areas, because they are relatively non-destructive, cost effective and not limited by depth (see Cappo et al. 2003 for review, Westera et al. 2003, Denny & Babcock 2004, Denny et al. 2004).

Over recent years the image quality of video has improved, and the initial capital investment has decreased sufficiently that it is now affordable for researchers to deploy multiple remote underwater video stations (RUVS) simultaneously, which greatly increases the potential replication and spatial coverage of sampling. Remote video sampling is non-extractive and, unlike research trawling, has minimal impacts on benthos. This allows information to be repeatedly gathered in protected areas in an acceptable manner. Remote underwater video stations can be accurately deployed into very rugose habitats, such as boulder fields, coral and limestone reefs, kelp and seagrass beds. The deployment and retrieval of a small frame influences the fish assemblages present for up to 4 min after deployment and retrieval in some habitats. The deployment of a small frame causes only small, localised habitat damage in fragile environments and does not harm the target fauna.


It might be predicted that samples from baited RUVS may be biased towards predatory or scavenging species and exclude herbivorous or omnivorous species. For example, striking differences have been recorded in catches from baited and unbaited fish traps (Newman 1990). Such dynamics would severely bias the discrimination of fish assemblages in temperate and tropical biodiversity surveys using RUVS methods.

This study compares the ability of baited and unbaited RUVS to discriminate among fish assemblages inhabiting distinct benthic habitats in shallow shelf waters of temperate and tropical Australia. We also explored the potential bias of using bait as an attractant by testing for differences in the diversity ($N_{sp}$) and relative abundance (MaxN) of fishes belonging to different trophic groups recorded by baited and unbaited RUVS.

METHODS AND MATERIALS

Temperate sampling. Four baited and 4 unbaited RUVS were deployed in each of 6 benthic habitats (a total of 48 samples) within Esperance Bay, South Western Australia (34° S, 122° E) in September 2002. The locations of deployments were selected from a habitat map of benthic coverage in the area. The 6 habitat categories sampled were: seagrass beds (SG), *Ecklonia radiata* macroalgal beds (Eck), other macrophytes (OM), deep reef (DR), rhodolith beds (Rhod) and sand (S). The seagrass habitat was characterised by a 60 to 100% cover of *Posidonia* spp. between depths of 10 and 16 m. *Ecklonia* and other macrophyte habitats were found on sloping granite reefs between depths of 3 and 28 m and had a 60% cover or greater of the small kelps *Ecklonia radiata* (Eck), or *Sargassum* spp. and *Cystophora* spp. (OM). Deep reefs comprised reefs of granite bedrock at depths >30 m, and were characterised by a sparse cover of macroalgae or sponges. Rhodolith and sand habitats had low relief, with an 80% or greater cover of rhodoliths or sand, and were always deeper than 30 m.

Within each habitat, four 1 h recordings were made for both baited and unbaited RUVS. At a site, unbaited and baited RUVS were set in a sequence, with unbaited RUVS being deployed first. We allowed 20 min to elapse before baited deployments were made at the same site. This minimum time was based on results from a prior study (E. Harvey unpubl. data), which showed that deploying and retrieving the camera system influenced the fish assemblages present for up to 4 min after deployment and retrieval in some habitats. Sampling was completed between 08:30 and 15:30 h to avoid crepuscular changes in fish behaviour. Up to 4 RUVS were deployed at any one time, at a separation of at least 500 m between stations to minimise the possibility of attraction of individual fish from one RUVS to another. Recordings were made using 4 stereo-video systems (see Harvey & Shortis 1996 and Harvey et al. 2002a for design and measurement procedures), using either Sony TRV900E or TRV15 digital camcorders within waterproof housings. Bait arms made of 20 mm plastic conduit with a standard rock lobster bait canister fastened to one end were attached to the stereo-video...
frame and detached during and after deployment (see Watson et al. 2005 for a description). The bait canister was approximately 1.25 m from the cameras. We used 1 kg of crushed South American pilchards Sardinops sagax placed in the bait bag for each deployment of baited RUVS. Unbaited RUVS also had a conduit and bait bag attached to the frame, but used clean bait canisters that had never had bait placed in them. Fish could be identified at up to 7 m from the cameras. At this distance we had a horizontal field of view with stereo coverage of 14.59 m and sampled an area of 51 m².

**Tropical sampling.** Six single camera RUYSs were deployed about 300 to 450 m apart along transects within habitat types in an alternating sequence of baited and unbaited units. The distance between sequential tropical stations was slightly less than temperate stations because they were set around reefs and in channels along the tracks of towed video cameras where the benthos was known. These tracks were relatively short and did not allow wider separation of the 6 stations. The stations consisted of a galvanized roll-bar frame enclosing a simple camera housing made from PVC pipe with acrylic front (dome) and rear ports. Stabilizing arms and arm ports (20 mm plastic conduit) were attached during deployment. The bait arm had two 50 mm square scale grids at both ends of a 350 mm plastic mesh bait canister containing 1 kg of crushed pilchards Sardinops neopilchardus (see Cappo et al. 2004 for diagram). Sony Hi-8 Handicams (Model TR516E) with wide-angle lenses (Hama 0.5×) were used in the housings.

Deployments (1 h) of baited and unbaited RUYSs were made in the central section of the Great Barrier Reef Marine Park (around latitude 18° S) near Calliope and Curacoa Channels in the Palm Islands, at Robbery Shoals offshore from the Palm Islands, and around the mid-shelf reefs and shoals of Rib Reef, Keels Shoals and Davies Reef. The habitat types were mapped prior to deployment of the RUYSs by use of a towed underwater television camera linked to a GIS, and were checked directly from the field of view of the video stations. The habitat categories recognised were: ‘megabenthos’ (including macroalgal beds, corals, sponge and gorgonian gardens; 26 to 36 m), ‘fine sand’ (including mud; 17 to 36 m), ‘coarse sand’ (including rubble; 27 to 47 m) and ‘near benthos’ (30 to 40 m). The ‘near benthos’ category covered sets where the RUYSs landed on sand, but significant patches of ‘megabenthos’ were seen in the field of view on the seabed, or during the deployment or retrieval. We deployed 6 baited and 6 unbaited RUYSs in each habitat.

**Analysis of video tapes.** Tape analysis commenced when the RUYSs settled on the seabed. For each species seen in both tropical and temperate RUYSs we recorded the maximum number seen together at any one time on the whole tape (MaxN). We used MaxN as a conservative estimator of the number of fish seen on a RUYS drop, because we were concerned that individual fish might be counted repeatedly when leaving and then re-entering the field of view during tape analysis. The MaxN of our study is the same as the $p_{\text{peak}}$ of Priede et al. (1994), the MAXNO of Ellis & DeMartini (1995) and the MAX of Willis & Babcock (2000). This estimator will result in separate visits by different individuals of the same species to a RUYS being recorded as MaxN = 1. MaxN will give conservative estimates of abundance in high-density areas. Therefore, any differences detected between treatments are also likely to be conservative (Willis et al. 2000, Cappo et al. 2003).

**Trophic groups.** All species of fish and elasmobranchs recorded on RUYS drops were assigned to 1 of 10 trophic groups, based on their feeding habits and functional morphology. This information was derived from ‘FishBase’ (Froese & Pauly 2006), and local fish identification guides. The groups were classified by the predominance of prey types into (1) ‘herbivores’, (2) ‘corallivores’, (3) ‘zooplanktivores’, (4) ‘piscivores’ and (5) ‘invertebrate carnivores’. Further groupings were recognised by the predominance of food in mixtures into (6) ‘algae/invertebrates’, (7) ‘invertebrates/algae’ and (8) ‘sponges/invertebrates’. Carnivores were also classified by the size and range of items eaten. (9) ‘Macro-invertebrate carnivores’, like larger rays, eat large items such as cephalopods, molluscs and crustaceans. (10) ‘Generalist carnivores’ were recognised on the basis of a wide range of fishes and invertebrates taken from various positions in the water column. Very large ‘generalist macrocarnivores’, such as larger sharks, were incorporated into the ‘generalist carnivore’ group because of their rarity in video records.

**Statistical analysis.** We used a 2-way non-parametric multivariate analysis of variance (PERMANOVA) (Anderson 2001, Anderson & Robinson 2003, Anderson & Gorley 2007) to test for differences in the fish assemblages sampled by baited and unbaited RUYSs. For the temperate data our experimental design consisted of 2 factors: ‘bait treatment’ (Treatment; 2 levels, fixed) and ‘habitat’ (Habitat; 6 levels, fixed) with 4 replicates. We used the same model for tropical data, with the exception that habitat had 4 levels rather than 6 and we had 6 replicates. We transformed the data using $\ln(x + 1)$ and used a Bray-Curtis dissimilarity measure. For each term in the analysis, 4999 permutations of the raw data units were computed to obtain p-values. For the temperate assemblage data, we excluded a schooling carangid Pseudocaranx dentex from the analysis. This was because P. dentex was often recorded in schools resulting in $\text{MaxN}_i > 100$ (where $i$ represents the species), and this variance dominated the analysis.
We also analysed the effect of treatment after removing the effect of habitat and depth. We used PERMANOVA with a single factor (Treatment) with habitat and depth treated as covariables in the model. To investigate the proportion of variance that each of the variables (treatment, habitat and depth) contributed to the assemblage structure we undertook a distance-based multivariate analysis for a linear model (DISTLM) (Anderson & Gorley 2007) using forward selection.

To visually compare the assemblages identified by baited and unbaited RUVS, a plot of the principal co-ordinates for both temperate and tropical fish assemblages was constructed from a constrained canonical analysis of principal coordinates (CAP; Anderson & Robinson 2003, Anderson & Willis 2003). We also tested for differences in the numbers of individuals and the numbers of species amongst treatments, and used non-parametric multivariate analysis of variance (PERMANOVA) (Anderson & Millar 2004) due to the predominance of zeros and the variability between samples. This analysis does not assume normality or any other specified distribution. We have analysed the data using the model described above (4999 permutations), but, because we used only one variable at a time, the analysis was based on Euclidean distance (Anderson & Millar 2004). For both the temperate and tropical data sets, we also analysed the numbers of individual fish (calculated as the sum of MaxNi) and the numbers of species (Nsp) within each trophic group. The aim of this analysis was to determine if particular trophic groups were influenced more by bait, and if the use of bait attracted more species and more individuals. Eight of the 10 trophic groups were recorded in the temperate data, and 10, in the tropical data.

RESULTS

The temperate and tropical video samples produced a diverse species list, ranging from small pomacentrids of <3 cm length to large sharks and rays of several metres in length. In 48 temperate samples, we recorded 1656 individuals from 63 species and 32 families. By contrast in the 48 RUUVS set in the tropics, we recorded 1548 individuals from 211 species and 37 families.

Assemblage data

In both the temperate and tropical regions, there were significant differences in the fish assemblages recorded by baited and unbaited RUUVS (Table 1). Significant differences between habitats were also recorded as a recurring theme throughout our results, but will not be interpreted here, as they are the focus of the analysis and interpretation of more comprehensive data sets. In the tropical data set, there was a significant Treatment × Habitat interaction (Table 1). This was caused by the lack of significant differences in the fish assemblages sampled by baited and unbaited RUUVS in coarse sand and near benthos habitats, combined with the significant differences detected amongst assemblages detected in fine sand and megabenthos habitats.

Treatment was still a significant effect after extracting the effect of habitat and depth for both temperate (Treatment1,47, MS = 10 140, pseudo-\(F = 5.48, p < 0.001\)) and tropical (Treatment1,86, MS = 8636.3, pseudo-\(F = 2.197, p = 0.003\)) data. In both analyses, the covariables were significant (\(p < 0.001\)). The DISTLM analysis revealed that treatment, habitat and depth all had significant influences on the structure of the fish assemblages sampled. For the temperate data, depth accounted for 15.4% of the variance, habitat for 11.5% and treatment for 8.1%. For the tropical data, depth accounted for 3.4% of the variance, habitat for 6.35% and treatment for 3.3%.

Plots of the principal co-ordinates from a CAP analysis for both temperate (Fig. 1A) and tropical (Fig. 1B) fish assemblages show that the use of bait allows greater discrimination between samples taken from different habitats, whilst increasing the similarity of samples taken within the same habitats. This was supported by the ‘leave one out’ allocation success (Anderson & Willis 2003) for both temperate and tropical fish assemblages, which provides a statistical estimate of mis-classification error and demonstrates how distinct groups of sites or samples are in multivariate space (Anderson & Willis 2003). Temperate assem-
blages had an allocation success of 54% with unbaited RUVS, which improved to 62.5% with bait. Tropical assemblages had an allocation success of 62.5% without bait, but 83% with bait.

**Numbers of individual fish and species sampled by baited and unbaited RUVS**

In both the temperate and tropical regions, there were significant differences in the numbers of individual fish (Table 2) and the numbers of species (Table 3) recorded by baited and unbaited RUVS. Significant differences amongst habitats were also recorded. Plots of the mean Max\(N_i\) (Fig. 2A) and mean number of species \(N_{sp}\) (Fig. 2B) show that overall greater numbers of individuals and species were recorded by baited than unbaited RUVS in both temperate and tropical marine habitats.

**Temperate trophic groups**

A 2-way non-parametric multivariate analysis of variance (PERMANOVA) showed that statistically significant higher mean numbers of individuals (Max\(N_i\); Fig. 3A) and species (\(N_{sp}\); Fig. 3B) were recorded by baited RUVS for 5 of the 8 trophic groups (piscivores, generalist carnivores, macroinvertebrate carnivores, invertebrate carnivores and invertebrate/algae feeders).

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**Table 2.** PERMANOVA of ln(x +1)-transformed abundance data for the number of individual fish sampled by baited and unbaited RUVS in 6 benthic habitats in temperate waters and 4 benthic habitats in tropical waters. Results are based on Euclidean distance. Definitions and abbreviations, see Table 1. **Bold values:** \(p < 0.05\)

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
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<tbody>
<tr>
<td><strong>Temperate</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>1</td>
<td>15.450</td>
<td>17.453</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>H</td>
<td>5</td>
<td>5.685</td>
<td>6.422</td>
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<td></td>
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<td></td>
</tr>
<tr>
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<td>&lt;0.001</td>
</tr>
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<td>H</td>
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<td>5.543</td>
<td>0.003</td>
</tr>
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<td>0.030</td>
<td>0.045</td>
<td>0.987</td>
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<tr>
<td>Total</td>
<td>47</td>
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</table>

**Table 3.** PERMANOVA of ln(x +1)-transformed data for the maximum number of species sampled by baited and unbaited RUVS in 6 benthic habitats in temperate waters and 4 benthic habitats in tropical waters. Results are based on Euclidean distance. Definitions and abbreviations, see Table 1. **Bold values:** \(p < 0.05\)

<table>
<thead>
<tr>
<th>Source</th>
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<th>F</th>
<th>p</th>
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<tr>
<td>T</td>
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<td>325.521</td>
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<td>H</td>
<td>5</td>
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<td>17.945</td>
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<td>6.121</td>
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<tr>
<td><strong>Tropical</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>T</td>
<td>1</td>
<td>2.277</td>
<td>9.379</td>
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</tr>
<tr>
<td>H</td>
<td>5</td>
<td>2.879</td>
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<td>T × H</td>
<td>5</td>
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ers, see Table 4, Fig. 3A,B) in comparison to unbaited RUVS. For both Max\(N_i\) and \(N_{sp}\), there were significant differences between habitats for all trophic groups, with the exception of piscivores and macroinvertebrate carnivores. There were significantly more individual generalist carnivores recorded in baited than unbaited RUVS.

There was also a significant Treatment × Habitat interaction for herbivores caused by a greater number of species and individuals of herbivorous fish recorded with bait in seagrass in comparison to other combinations of habitat and treatment. However, overall numbers of herbivores seen were low, and this outcome must be treated with caution.

**Tropical trophic groups**

In the tropical data, a 2-way non-parametric multivariate analysis of variance (PERMANOVA) showed significantly higher mean numbers of individuals (Max\(N_i\); Fig. 4A) and species (\(N_{sp}\); Fig. 4B) were recorded by baited RUVS for piscivores, generalist carnivores and invertebrate carnivores in comparison to unbaited RUVS (Table 5, Fig. 4A,B). For Max\(N_i\) there were significant differences between habitats for 6 of the 10 trophic groups (exceptions being generalist carnivores, macroinvertebrate carnivores, corallivores and invertebrates/algae). A similar pattern was seen for \(N_{sp}\) with no significant differences recorded be-
between habitats for the macroinvertebrate carnivores, corallivores and invertebrates/algae trophic groups.

There was also a significant Treatment × Habitat interaction for macroinvertebrate carnivores for Max \( \text{Ni} \) and \( N_{sp} \), with more individuals and species being recorded in unbaited RUFS in near benthos habitats. Similarly, with invertebrates/algae, a Treatment × Habitat interaction was caused by a greater number of individuals being recorded in unbaited RUFS in coarse sediments.

**DISCUSSION**

The use of bait increased the ability of RUFS to discriminate fish assemblages in distinctive benthic habitats in tropical and temperate Australia. This was due to the increased numbers of individuals and species sampled at the baited stations. Similarly, there were also increasing trends evident in the number of species and individuals in approximately half of the trophic groups, which is contrary to the expectations from previous trapping studies (Munro 1974).

This is an important outcome for researchers interested in assessing demersal fish biodiversity.

Fish trapping studies have shown that herbivorous siganids and scarids dominate catches of unbaited traps on coral reefs, yet these families seldom appear in baited traps (Munro 1974, Newman 1990). Furthermore, it could be argued that the predators and scavengers attracted to the baited fish traps or RUFS might interact with non-predatory or herbivorous species, resulting in a reduced number of individuals, species and trophic groups being recorded. Of particular interest in our study is the finding that there was no statistically significant difference between the baited and unbaited RUFS for the numbers and diversity of fish sampled in the herbivorous or invertebrate/algae trophic groups. The use of bait did not deter fish from these trophic groups being recorded in the field of view. Instead, baited RUFS sampled more herbivorous species in temperate and tropical habitats and more individuals in tropical habitats (Max \( \text{Ni} \) for herbivores was identical in temperate habitats) than the unbaited RUFS. This is an important finding that contradicts the outcomes of some trapping studies, which have found that relative abundances of herbivorous fish decrease when bait is set as a fish attractant.

Our observations of fish behaviour during the tape analysis showed that herbivorous species did not readily approach the camera or the bait canister, but

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**Table 4. Temperate assemblage: the results of PERMANOVA tests for differences in numbers of individuals (Max \( \text{Ni} \)) and species (\( N_{sp} \)) between baited and unbaited RUFS (T: treatment) for trophic groups in 6 habitats (H); \( N = 4 \) baited and 4 unbaited RUFS per habitat. Bold values: \( p < 0.05 \)**

<table>
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<th>Source</th>
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<th>Individuals (Max ( \text{Ni} ))</th>
<th>Species (( N_{sp} ))</th>
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<tr>
<td></td>
<td></td>
<td>MS</td>
<td>( F )</td>
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<tr>
<td><strong>Piscivore</strong></td>
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<tr>
<td>T</td>
<td>1</td>
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<td>Total</td>
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<td><strong>Generalist carnivore</strong></td>
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<td>T</td>
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Table 5. Tropical assemblage: the results of PERMANOVA tests for differences in the numbers of individuals (MaxN) and species (Nsp) between baited and unbaited RUVS (T: treatment) for trophic groups in 4 habitats (H); N = 6 baited and 6 unbaited RUVS per habitat. Bold values: p < 0.05.

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</table>
biases associated with baited RUVS are to compare the technique with underwater visual census (UVC) by divers in shallow waters (Willis et al. 2000, Watson et al. 2005) and with common extractive techniques in deeper waters, such as trawling (e.g. Priede & Merrett 1996, Cappo et al. 2004), long-lining (Ellis & DeMartini 1995) and trapping. In this way, Watson et al. (2005) showed that bait increased the sampling power of RUVS, and that use of UVC and baited RUVS supplemented the overall assessment of biodiversity.

One of the key issues yet to be addressed by users of baited RUVS in continental shelf waters is the distance over which fish may be attracted to the bait. Studies using baited RUVS targeting deepwater scavengers (e.g. Priede & Merrett 1996) have modelled the area of attraction using MaxN and arrival time, in conjunction with knowledge of current velocities, fish swimming speeds and models of bait plume behaviour, to estimate absolute density. These numerically sophisticated approaches require a number of unverifiable assumptions, and results are not amenable to robust falsification. In contrast, users of baited RUVS on shelf and coastal reefs have ignored plume dispersal, and utilised various calibrations of abundance indices during short sets (10 to 90 min) to estimate patterns of relative abundance (e.g. Ellis & DeMartini 1995, Willis & Babcock 2000). However, some attempts have been made to avoid overlap of the plumes among baited RUVS, to ensure that replicates are independent of one another (see Cappo et al. 2004).

Different types of bait may influence the numbers of individuals and species attracted to the bait and the distance over which a fish is attracted. The effect of bait type in RUVS can be inferred from previous studies on the catch rates of fish traps and baited hooks. Oily, soft-fleshed baits, such as clupeid baitfish, are clearly superior (4 to 5 times more effective) to white-fleshed baits (Whitelaw et al. 1991) and octopus (High 1980), in terms of attractiveness to fish. Similarly, the probability of arrival of a fish at the baited trap or hook has been reported to be governed by the size, type and freshness of the bait, and the search pattern, appetite and response time of the fish (e.g. Miller 1983, Lokkeborg & Bjordal 1992). Therefore, if baited RUVS are to be used for sampling involving temporal or spatial comparisons then the type of bait, the quantity of bait used and delivery should be standardised. Seasonal, reproductive and lunar patterns of activity in the swimming speed, schooling behaviour and appetite of the fish presumably also affect the attraction of fish to a bait, as will conspecific attraction, curiosity, the presence or absence of predators and home range sizes (Munro 1974, Newman 1990).

The results presented here indicate that baited remote underwater video stations (BRUVS) are capable of recording fishery-independent data on demersal fish assemblages that is robust and reproducible. If standardised camera designs, field techniques (including bait type and quantity) and video analysis techniques are used, future studies should be comparable spatially and temporally, even if collected by different research groups. The key challenge is ensuring that the areas or volumes within which fish are counted are defined and consistent, requiring the use of stereo-video techniques (Harvey et al. 2004).

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Ellis DM, DeMartini EE (1995) Evaluation of a video camera technique for indexing the abundances of juvenile pink
snapper, *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes. Fish Bull (Wash DC) 93:67–77

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INTRODUCTION

Pelagic fish are often overlooked during the design and implementation of marine protected areas (MPAs) and during subsequent monitoring programs. However, increases in the biomass of carangids and other large predatory fish have been reported in MPAs in Hawaii and the Philippines (Russ & Alcala 1996, Williams et al. 2006), suggesting that pelagic fish may benefit from MPA protection. Designing MPAs to maximize protection for pelagic species, and monitoring changes after implementation, requires knowledge of pelagic distributions and habitat preferences. Conservation and monitoring programs based on accurate survey data are becoming increasingly urgent, as many pelagic species have experienced serious stock declines (Cury et al. 2000, Myers & Worm 2003).

Pelagic fish behaviour presents difficulties for the collection and interpretation of accurate survey data. High spatial and temporal variability in pelagic fish distribution and abundance means that traditional fish survey techniques, when applied to pelagic fish assemblages, assessed using mid-water baited video: standardising fish counts using bait plume size

Elizabeth C. Heagney1,*, Tim P. Lynch2, Russ C. Babcock3, Iain M. Suthers1

1School of Biological Earth and Environmental Science, University of New South Wales, Sydney, New South Wales 2052, Australia
2Jervis Bay Marine Park, PO Box 89, Huskisson, New South Wales 2540, Australia
3CSIRO Marine Research and Atmospheric Research, Private Bag No 5, Wembley, Western Australia 6913, Australia

ABSTRACT: We used a novel mid-water baited remote underwater video (BRUV) technique to survey pelagic and mid-water fish assemblages at Lord Howe Island Marine Park, off eastern Australia (31.5°S, 159.1°E). We found differences in assemblages among regions separated on a scale of ~10s of kilometres. Of the environmental variables measured in the present study (depth, temperature, water current speed), current speed had the greatest influence on the structure of pelagic assemblages. Carcharhinus galapagensis, Seriola rivoliana and Scomber australasicus had similar distributions and were associated with low flow environments. Seriola lalandi was associated with the higher flow environments sampled during our surveys, although current speeds in the sample area were relatively low (0.03 to 0.34 m s⁻¹; mean 0.17 m s⁻¹). Relationships between pelagic assemblages and current speed were detected when abundances were calculated using an area-based approximation for plume dispersal, but were not detected using a linear approximation, or when current was assumed constant across all BRUV deployments. Our results demonstrate the difficulty in separating the dual effects of current speed in BRUV studies: the effect of current on bait plume size and associated estimates of fish abundance, and the role of current as an aspect of preferred pelagic fish habitat. We recommend the use of area-based approximations of plume dispersal and the inclusion of accurate estimates of current speed as a statistical covariate when interpreting mid-water BRUV data. Our results indicate that oceanographic characteristics can be important for pelagic fish habitat selection over the scale of kilometres and should be considered during marine protected area zoning.

KEY WORDS: Marine protected area (MPA) · No-take sanctuary zone · Shark · Galapagos whaler · Oceanography · Carangidae · Carcharhinidae · Lord Howe Island

1 Email: e.heagney@unsw.edu.au © Inter-Research 2007 · www.int-res.com

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assemblages, often yield patchy data, with many zeros and limited statistical power (Edgar & Barrett 1999, Kingsford 1999). Pelagic fish are also fast swimmers that can avoid survey equipment including nets, boats and SCUBA divers (Freon & Misund 1999, Misund et al. 1999). As a result of these difficulties, pelagic fish research is often reliant on fisheries data, with attendant sampling biases (Gillanders et al. 2001). Fisheries data are also inappropriate for studies in MPAs, where fishing is often banned.

Baited remote underwater video (BRUV) has successfully been used to survey fish assemblages in a number of ecosystems, including shallow coastal reefs (Ellis & DeMartini 1995, Babcock et al. 1999), continental slopes (Collins et al. 1999a, Speare et al. 2004) and deep abyssal plains (Wilson & Smith 1984, Friede & Merrett 1998). BRUV also shows potential to overcome difficulties associated with surveying open-water ecosystems, as pelagic fish have been observed during benthic BRUV surveys (Jones et al. 2003, Cappo et al. 2004, Watson et al. 2005). The use of bait to attract fish to survey gear overcomes problems associated with gear avoidance, as most pelagic fish are opportunistic predator/scavengers that respond to bait plumes (Bozzano & Sardà 2002, Jones et al. 2003). Using a remote video system also eliminates problems of fish avoiding or being attracted to the research vessel. BRUV has the additional advantage of supplying behavioural data, and insights into inter- or intra-specific interactions (Bozzano & Sardà 2002, Jones et al. 2003, Collins et al. 2005, Kemp et al. 2006), that may boost our understanding of the structure and function of pelagic ecosystems.

Applying BRUV to mid-water environments requires reconsideration of some of the assumptions in BRUV studies. For example, many BRUV studies assume that each deployment samples an equivalent area by either ignoring water current speed, or by using the average current speed from all deployments to estimate the area sampled by each BRUV (e.g. Hill & Wassenberg 1999, Henriques et al. 2002, Jones et al. 2003). This may be a reasonable assumption when baits are deployed into the bottom layer where currents are damped by frictional forces, but when baits are deployed into mid-water environments or the surface mixed layer, variable current speeds and turbulent mixing will cause relatively large differences in the area sampled by the bait plume in each BRUV deployment. In such environments it may be more realistic to use in situ measurements of current speed for each BRUV deployment and to include horizontal and/or vertical mixing terms when estimating bait plume area or volume (Sainte-Marie & Hargrave 1987).

We investigate how different assumptions about bait plume dispersal affect estimates of pelagic fish abundance and, particularly, how variations in current speed can influence regional comparisons, assessments of habitat preferences and MPA monitoring. We present findings from mid-water BRUV sampling on the continental shelf around Lord Howe Island, a remote island in the central Tasman Sea, east of Australia. The waters surrounding this small volcanic island provide a rare opportunity to investigate the ecology and behaviour of pelagic fish assemblages, because large-scale commercial fishing efforts targeting pelagic species have always been absent from the region (NSW MPA 2000, NSW DPI 2004). Of particular interest is the regional abundance of tropical sharks, many species of which have been subject to severe over-fishing throughout their range (Ovetz 2006).

**MATERIALS AND METHODS**

**Study site.** Lord Howe Island is an isolated volcanic island approximately 630 km east of Australia (31.5° S, 159.1° E; Fig. 1). The island is surrounded by continen-

![Fig. 1. Chart of Lord Howe Island and Balls Pyramid showing marine park zoning and sampling regions: 1: Admiralty Islands; 2: Red Point/Clear Place; 3: Wolf Rock shoals/the Triangle; 4: Balls Pyramid/South East Rock. Asterisk in Region 4 indicates the location of a small sanctuary zone not visible at the scale of the map provided. Arrow indicates the direction of prevailing current during the survey period.](image-url)
tal shelf, approximately 10 km wide, with maximum depth ~100 m. Balls Pyramid, a second, smaller island with similar continental shelf structure, is located approximately 25 km south-east of the main island (Fig. 1). Lord Howe Island is surrounded by the cool waters of the Tasman Sea and is seasonally encircled by the warm East Australian Current (EAC) (Boland & Church 1981). Water temperatures at the time of sampling (22.2 to 23.2°C) and satellite data (BLUElink www.cmar.csiro.au/bluelink) indicate that EAC waters dominated throughout our study period, and prevailing currents were from the NNW. The waters extending 3 nautical miles around Lord Howe Island and Balls Pyramid were declared an MPA in 1999, and a multiple-use zoning plan was implemented in December 2004 (NSW MPA 2004), just 5 mo before our study. Under the plan, 27% of the waters surrounding Lord Howe, or 12,500 ha, became sanctuary zone where all extractive uses are prohibited (Fig. 1).

**Sampling design.** Mid-water BRUVs were deployed at multiple sites in 4 regions of the continental shelf of Lord Howe Island and Balls Pyramid (Fig. 1): the Admiralty Islands, comprising a group of 6 smaller islands just north of Lord Howe Island proper (Region 1); Red Point/Clear Place, located on the east coast of the main island (Region 2); Wolf Rock shoals/the Triangle, 2 submerged seamounts off the east coast of the island (Region 3); and Balls Pyramid/South East Rock (Region 4). Regions were separated on a scale of ~10s of kilometres, and were chosen in consultation with local recreational and charter boat fishers as areas where pelagic fish are (or have historically been) targeted by either boat-based trolling or rock fishing. Sample regions were also chosen to include both MPA sanctuary zones and areas that have remained open to fishing. A total of 50 BRUV deployments were conducted during the period from 26 March to 9 April 2005. We conducted 10 to 20 replicate deployments in each region, with deployments equally divided between fished areas and MPA sanctuary zones in each region. Where replicate deployments were conducted simultaneously within a region, these were separated on a scale of ~1.5 to 3 km. Based on maximum recorded current speeds of 0.34 m s⁻¹ and a deployment period of 45 min, we estimate the maximum linear extent of any bait plume was ~920 m and conclude that all BRUV deployments represent independent samples (Ellis & DeMartini 1995, Cappo et al. 2004).

**Mid-water BRUV design.** Each BRUV contained a Sony mini-dv camera (TRV 19E and HC 30E series) fitted with a wide-angle lens with a conversion factor of 0.6 (Fig. 2). Cameras were mounted inside custom-built PVC pipe housings, which were attached to a light aluminium frame, with a horizontal aspect to a small plastic bait container (13 cm length × 8 cm diameter) 1 m from the lens. PVC tubes (15 mm diameter) were attached to the frame at set intervals behind the bait container (0.5 and 1 m) as reference markers for fish size and distance from the camera. BRUV frames were designed to align in the current such that the cameras were always pointing down-stream, allowing fish to be observed swimming up-current into the bait plume. Frames were also designed so that all supports and reference markers were visible in front of the camera to ensure that any fish associating with these structures were visible in camera footage (Jamieson et al. 2006). Each BRUV was attached to a mooring, consisting of an anchor line, anchor, sub-surface buoy and surface buoy (Fig. 2). Video equipment was suspended at a depth of 10 m from the surface using elasticized bungee cord in order to reduce movement in response to wave action. Video equipment was baited using 100 g (±1 g) of a mixture of minced pilchards, bread and tuna oil (8:1:1), all bait components that are commonly used by pelagic fishers in eastern Australia. The mixture was combined in a matrix of vegetable meal (falafel) to ensure that bait release was continual over the deployment period and proportionate to local current speed. Mid-water BRUVs were deployed for 45 min. The research vessel moved well away from the sample sites to avoid confounding effects of fish associating with the vessel.
At each site we recorded depth, water temperature and current speed. Surface temperature was measured using temperature sensors mounted on the boat hull, and temperature at 10 m depth was measured using loggers attached to BRUV frames. These were compared to ensure all BRUVs were deployed into the surface mixed layer. Current speed was estimated upon collection of each BRUV using a drogue deployed to 10 m depth. As the surface buoy had drifted to the extent of its anchor line at the end of each BRUV deployment, it was considered a stationary point. The drogue was deployed next to the stationary buoy and attached to it via a 10 m line. We estimated current speed from the time taken for the drogue to travel to the extent of the 10 m line.

**Image analysis.** Pelagic and mid-water fish observed on video footage were identified to species. For each deployment we recorded Max\(N\), the maximum number of fish from each species seen in a single frame in the first 45 min of video footage (after Willis et al. 2000). Max\(N\) is a conservative estimate of the total number of fish present in the deployment area, because only a proportion of the fish that detect the bait plume will respond by moving up-current to the video equipment (Løkkeborg 1998), and because fish do not remain at the bait once they have been attracted; rather, they leave the field of view and re-visit the bait on a number of occasions (Kallayil et al. 2003). However, Max\(N\) was considered preferable to time-based measures like time to arrival of first fish or fish arrival rates (Sainte-Marie & Hargrave 1987, Bailey & Priede 2002), because these could be confounded by the patchy spatial distribution of pelagic fish schools, interactions between school size and foraging and swimming efficiency (Misund & Aglen 1992, Day et al. 2001), and potential association between target species and the research vessel (Dagorn et al. 2001, Meekan & Cappo 2004).

Visibility during our survey period was consistently good (>30 m), so all fish observed in video footage were included in Max\(N\). Rough size estimates were possible for *Carcharhinus galapagensis* individuals that swarm close and parallel to reference markers (Meekan & Cappo 2004, Kemp et al. 2006).

**Estimating fish abundance.** To investigate whether equations used in deep-sea baited camera studies for converting video indices to abundance estimates are applicable to mid-water BRUV data, we compared Max\(N\)/Plume with Max\(N\)/Attract. Max\(N\)/Plume calculates the abundance relative to the size of the bait plume at the completion of a 45 min deployment, while Max\(N\)/Attract calculates the abundance relative to the size of the bait plume at the latest time a fish could detect the plume and swim to the bait in time to be viewed in the first 45 min of video footage (Sainte-Marie & Hargrave 1987, Priede & Merrett 1996). We compare Max\(N\)/Plume\(_{\text{dist}}\) with Max\(N\)/Attract\(_{\text{dist}}\) for a linear approximation of bait plume dispersal where:

\[
\text{Plume}_{\text{dist}} = 45 \times 60 \times v_w
\]

and

\[
\text{Attract}_{\text{dist}} = 45 \times 60 / \left(\frac{1}{v_w} + \frac{1}{v_f}\right)
\]

and where \(v_w\) is current speed and \(v_f\) is fish swimming speed (m s\(^{-1}\); Priede & Merrett 1996). Comparisons were conducted for 4 pelagic species considered representative of the range of fish sizes and swimming capabilities observed in our study (Table 1). Published estimates of fish size and swimming speeds were used (Henriques et al. 2002). Where these were unavailable, published swimming speed data for a congener with a similar aspect ratio were used (Table 1). All estimates represent the maximum cruising speed reported for each species (Sainte-Marie & Hargrave 1987).

We also compared Max\(N\)/Plume\(_{\text{area}}\) with Max\(N\)/Attract\(_{\text{area}}\) for a triangular area approximation of bait plume dispersal (Sainte-Marie & Hargrave 1987, Hill &

---

**Table 1.** Mean maximum swimming speed estimates (m s\(^{-1}\)) for 4 pelagic species estimated from maximum swimming speed in body lengths (BL) per second and mean fish length (0.5 × maximum length reported in the literature). Where published data for observed species were unavailable, we have used maximum swimming speed of a congener with similar aspect ratio. FL: fork length

<table>
<thead>
<tr>
<th>Species</th>
<th>Surrogate</th>
<th>Max. speed (BL s(^{-1}))</th>
<th>Mean FL (m)</th>
<th>Max. speed (m s(^{-1}))</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Carcharhinus galapagensis</em></td>
<td><em>C. leucas</em></td>
<td>3.65</td>
<td>2.0(^{a})</td>
<td>7.3</td>
<td>Bainbridge (1958)</td>
</tr>
<tr>
<td><em>Seriola lalandi</em></td>
<td>–</td>
<td>2.30</td>
<td>1.0</td>
<td>2.3</td>
<td>Kuiter (2000), Clark &amp; Seymour (2006)</td>
</tr>
<tr>
<td><em>Paracaelus xanthus</em></td>
<td><em>Pristopomoides filamentosus</em></td>
<td>3.00</td>
<td>0.2</td>
<td>0.6</td>
<td>Kuiter (2000), Ellis &amp; DeMartini (1995)</td>
</tr>
<tr>
<td><em>Scomber australasicus</em></td>
<td><em>Sc. japonicus</em></td>
<td>4.50</td>
<td>0.3</td>
<td>1.4</td>
<td>Hutchins &amp; Swainston (1999), Nauen &amp; Lauder (2000)</td>
</tr>
</tbody>
</table>

\(^{a}\)Based on length estimates obtained from BRUV footage during the present study
Wassenberg 1999), assuming horizontal turbulent mixing occurred at a rate of one-third the current speed. We estimated $\text{Plume}_{\text{area}}$ as the area of a triangle with length $\text{Plume}_{\text{dist}}$ and height ($=0.33 \times$ length) and $\text{Attract}_{\text{area}}$ as the area of a triangle with length $\text{Attract}_{\text{dist}}$ and width ($=0.33 \times$ length). A scaling variable of $a$ was chosen as a conservative estimate of mixing given that current speeds in the sample area were relatively slow (0.03 to 0.34 m s$^{-1}$; mean 0.17 m s$^{-1}$) and that wave action on BRUVS enhanced bait dispersion. Vertical mixing, which is likely to be substantial in the surface mixed layer, has been excluded from our model. Based on our comparisons (see ‘Results’), we conducted all further analyses using $\text{Max} N$, $\text{Max} N/\text{Plume}_{\text{dist}}$ and $\text{Max} N/\text{Plume}_{\text{area}}$.

**Identifying pelagic fish habitat.** Pelagic and mid-water fish assemblages, comprising the 6 most abundant species attracted to baits, were compared using a 2-factor, full-factorial ANOVA design with the factors Zone (fished versus sanctuary; fixed) and Region (random). Comparisons were conducted using DISTLM (Anderson 2001, McArdle & Anderson 2001). Data were fourth-root transformed to minimize the influence of highly abundant or schooling species, and Bray-Curtis dissimilarity matrices were used. High sighting rates of *Carcharhinus galapagensis* enabled similar analyses to be conducted on abundance data for this species; again abundance data were square-root transformed. DISTLM was used also to perform permutational regression between pelagic assemblages and environmental variables (water current speed, temperature, depth) and to compare environmental variables among sample regions and MPA zones. On the basis of our results, all DISTLM analyses were repeated with current speed as an included covariate. Each of the above analyses was conducted using $\text{Max} N$, $\text{Max} N/\text{Plume}_{\text{dist}}$ and $\text{Max} N/\text{Plume}_{\text{area}}$ in order to investigate how assumptions about bait plume dispersal affected results. Associations between pelagic species were determined using principal components analysis of $\text{Max} N/\text{Plume}_{\text{area}}$ abundance data, with varimax rotation.

**RESULTS**

**Pelagic fish assemblages around Lord Howe Island**

Mid-water BRUV surveys identified 11 pelagic or mid-water species from 5 families: Carangidae, Carcharhinidae, Kyphosidae, Lutjanidae and Scombridae (Table 2). Of these, 7 species were abundant and observed on multiple occasions at a variety of sample sites, while the remaining 4 were observed only once. Several pelagic or mid-water species, including *Seriola lalandi*, *Pseudocaranx dentex*, *Kyphosus sydneyanus* and *Paracaelus xanthus*, were often observed in schools of 10s of individuals. Two different colour forms of *P. dentex* were observed during video surveys: those with grey or white-tipped dorsal fins, which are common along the NSW coast and a second yellow-finned variant (Hutchins & Swainston 1999). All *Kyphosus bigibbus* individuals observed were of the less-common, all-yellow colour variant described by Myers (1999), and were observed in mixed schools with *K. sydneyanus*.

The most commonly observed species during BRUV sampling was *Carcharhinus galapagensis*, which was observed on 80% of video deployments. A single individual from a second carcharhinid species, *Galeocerdo cuvier*, was also observed. All *C. galapagensis* whose lengths were estimated were juveniles, ranging from

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Common name</th>
<th>Individuals (no.)</th>
<th>Sightings (no.)</th>
<th>Max. school size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carangidae</td>
<td><em>Carcharhinus galapagensis</em></td>
<td>Galapagos whaler</td>
<td>111</td>
<td>40</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td><em>Galeocerdo cuvier</em></td>
<td>Tiger shark</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Carangidae</td>
<td><em>Seriola lalandi</em></td>
<td>Yellowtail kingfish</td>
<td>79</td>
<td>12</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td><em>Seriola rivoliana</em></td>
<td>Highfin amberjack / almaco jack</td>
<td>10</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><em>Pseudocaranx dentex</em></td>
<td>White trevally / silver trevally</td>
<td>121</td>
<td>8</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td><em>Caranx sp.</em></td>
<td>Trevally sp.</td>
<td>3</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Kyphosidae</td>
<td><em>Kyphosus sydneyanus</em></td>
<td>Sydney drummer</td>
<td>77</td>
<td>9</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td><em>Kyphosus bigibbus</em></td>
<td>Grey sea chub</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lutjanidae</td>
<td><em>Paracaelus xanthus</em></td>
<td>Southern fusilier / painted lady</td>
<td>988</td>
<td>20</td>
<td>200</td>
</tr>
<tr>
<td>Scombridae</td>
<td><em>Scomber australasicus</em></td>
<td>Blue mackerel / slimy mackerel</td>
<td>37</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td><em>Acanthocybium solandri</em></td>
<td>Wahoo</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 2. Pelagic species observed using mid-water BRUV (baited remote underwater video), number of individuals sighted, number of deployments (out of 50) on which sightings were made and maximum school sizes. Individuals from 12 additional ‘reef fish’ families were also observed: Acanthuridae, Balistidae, Chaetodontidae, Dasyatidae, Fistulariidae, Girellidae, Labridae, Lethrinidae, Microcanthidae, Monocanthidae, Pomacentridae, Serranidae
~1.2 to ~2 m in length. On 12 occasions we observed behavioural associations between *C. galapagensis* and other pelagic fish, where fish followed closely behind individual sharks, usually within 1 m, and mirrored shark swimming and turning patterns. Behavioural associations between *C. galapagensis* and the small pelagic *Scomber australasicus* were observed on 6 occasions; associations between *C. galapagensis* and other large pelagic fish (*Seriola lalandi*, *Seriola rivoliana*, *Pseudocaranx dentex*) were also observed on 6 occasions.

**Estimating fish abundance**

Most pelagic and mid-water fish were observed arriving at BRUVs from downstream of the bait, indicating that chemosensory cues from the bait plume were a more important attractant than boat noises, structural complexity of BRUV frames, or other cues (Wilson & Smith 1984, Sainte-Marie & Hargrave 1987, Collins et al. 1999a). Exceptions were *Kyphosus sydneyanus* and *K. bigibbus*, which showed no directional patterns in arrival. These species were excluded from further analyses as converting MaxN to abundance based on plume dynamics was considered inappropriate and likely to confound assemblage patterns.

**Identifying pelagic fish habitat**

We detected regional differences in pelagic fish assemblages (Table 3). Highest pelagic fish abundances were observed in Region 1; high abundances of *Seriola lalandi* and *Pseudocaranx dentex* in Region 1 related to multiple sighting of relatively large schools (school sizes n = 30 and n = 34 for *S. lalandi*, n = 50 and n = 60 for *P. dentex*). Lowest pelagic fish abundances were observed in Region 2, and moderate abundances were observed in Regions 3 and 4 (Fig. 3). *Carcharhinus galapagensis*, *S. lalandi* and *Paracaesio xanthurus* were common to all regions, *Scomber australasicus*

<table>
<thead>
<tr>
<th>Source</th>
<th>MaxN</th>
<th>MaxN/Plume&lt;sub&gt;dist&lt;/sub&gt;</th>
<th>MaxN/Plume&lt;sub&gt;area&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pelagic assemblages</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region</td>
<td>5191</td>
<td>2.37</td>
<td>0.01</td>
</tr>
<tr>
<td>Region (+current)</td>
<td>5508</td>
<td>2.63</td>
<td>0.006</td>
</tr>
<tr>
<td>Zone</td>
<td>2229</td>
<td>0.82</td>
<td>0.24</td>
</tr>
<tr>
<td>Zone (+current)</td>
<td>4334</td>
<td>1.56</td>
<td>0.26</td>
</tr>
<tr>
<td>Region × Zone</td>
<td>2735</td>
<td>1.25</td>
<td>0.22</td>
</tr>
<tr>
<td>Region × Zone (+current)</td>
<td>2569</td>
<td>1.23</td>
<td>0.27</td>
</tr>
<tr>
<td>Current</td>
<td>3670</td>
<td>1.59</td>
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</tr>
<tr>
<td>Depth</td>
<td>943</td>
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<td>0.81</td>
</tr>
<tr>
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<td>587</td>
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<td>0.90</td>
</tr>
<tr>
<td><em>C. galapagensis</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Region</td>
<td>4679</td>
<td>2.94</td>
<td>0.02</td>
</tr>
<tr>
<td>Region (+current)</td>
<td>4656</td>
<td>3.07</td>
<td>0.02</td>
</tr>
<tr>
<td>Zone</td>
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<td>3.77</td>
<td>0.03</td>
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<tr>
<td>Zone (+current)</td>
<td>7456</td>
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<tr>
<td>Region × Zone (+current)</td>
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<tr>
<td>Temperature</td>
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<td>0.32</td>
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</table>

MaxN/Plume<sub>dist</sub> and MaxN/Attract<sub>dist</sub> were highly correlated for the 4 species examined (R² > 0.99). Slopes of MaxN/Plume<sub>area</sub> versus MaxN/Attract<sub>area</sub> were close to 1 for fast-swimming species (1.02 for *Carcharhinus galapagensis*, 1.06 for *Seriola lalandi*) and were slightly higher for slower swimmers (1.18 for *Paracaesio xanthurus*, 1.13 for *Scomber australasicus*). Similar trends were observed for comparisons between MaxN/Plume<sub>area</sub> and MaxN/Attract<sub>area</sub>. Since MaxN/Plume does not incorporate errors associated with estimating fish swimming speed, we used MaxN/Plume (distance or area) for all subsequent analyses.

Table 3. Mean squares, pseudo F-statistic and permutation p-values from DISTLM analyses comparing pelagic fish assemblages and *Carcharhinus galapagensis* abundance across regions, marine protected area (MPA) zones and environmental variables. +current: current was included as a covariate in analysis. **Bold values:** p < 0.05
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was absent from Region 2, and *Seriola rivoliana* and *P. dentex* were absent from Regions 2 and 3 (Fig. 3). Similarities were observed for assemblages from Regions 3 and 4, while Regions 1 and 2 each contained distinct assemblages (Fig. 4a). No differences in assemblages were observed between fished areas and MPA sanctuary zones. Of the environmental variables measured, current speed had the greatest influence on pelagic fish assemblages (Table 3). *C. galapagensis*, *Seriola rivoliana* and *S. australasicus* were associated with areas of slower current speed, while *S. lalandi* was generally found at sites with faster current speeds (Fig. 4b).

Regional differences in abundance were also observed for *Carcharhinus galapagensis* (Table 3), which were most abundant in Region 3 and least abundant in Region 4 (Fig. 5a). *C. galapagensis* abundance was also higher inside MPA sanctuary zones compared with fished areas (Fig. 5b).

**Effect of bait plume assumptions**

An inverse correlation between *Carcharhinus galapagensis* abundance and current speed was detected using MaxN/Plume\textsubscript{area} (Table 3, Fig. 6). Current speed was also the most important environmental variable structuring pelagic fish populations (Table 3); again significant correlations between assemblage composition and current speed were only detected using MaxN/Plume\textsubscript{area}, although marginally significant differences were detected using MaxN/Plume\textsubscript{dist} (p = 0.057).

Differences in pelagic fish assemblages and *Carcharhinus galapagensis* abundance among regions and MPA zones were detected irrespective of the abundance index used (MaxN, MaxN/Plume\textsubscript{dist}, MaxN/Plume\textsubscript{area}; Table 3). However, sensitivity to differences changed depending on whether or not current speed was included as a covariate in DISTLM analyses. The inclusion of a current speed covariate made DISTLM...
more sensitive to differences among regions, but less sensitive to differences between fished areas versus sanctuary zones (Table 3). This result was related to systematic differences in current speed observed between fished areas and MPA sanctuary zones (Table 4). Over our 2 wk sampling period, significantly lower mean current speeds were recorded in fished areas compared with MPA sanctuary zones—a trend which was consistent across all 4 regions sampled (Fig. 7).

A marginally significant positive correlation was observed between current speed and temperature ($r = 0.06, p = 0.057$).

### DISCUSSION

**Pelagic and mid-water fish assemblages at Lord Howe Island**

Our novel mid-water BRUV surveys identified 11 pelagic and mid-water species, 7 of which were abundant and observed on numerous occasions in multiple regions. Surveys provided data on pelagic fish that are targeted or caught incidentally by local charter and recreational fishers (*Carcharhinus galapagensis*, *Seriola lalandi*, *S. rivoliana*, *Pseudocaranx dentex*), as well as un-fished pelagic and mid-water species (*Paracaelia xanthurus*, *Scomber australasicus*, *Kyphosus sydneyanus*, *K. bigibbus*), thereby providing important data on the structure of mid-water ecosystems not available through catch statistics. By far the most common species observed during our surveys was *C. galapagensis*. Sightings included numerous juveniles, although this may indicate a behavioural bias whereby juvenile sharks approach reference markers more
often and more closely. The presence of juveniles in the area indicates that the Lord Howe Island continental shelf may be a nursery area for this species, and is consistent with previous studies of _C. galapagensis_ that have found that juveniles are restricted to coastal, or relatively shallow, areas (Last & Stevens 1994, Wetherbee et al. 1996). BRUV surveys also provided useful qualitative data regarding behavioural associations between _C. galapagensis_ and other pelagic species. Large pelagic species may associate with _C. galapagensis_ to enhance camouflage, or due to some feeding advantage conferred by the superior detection and hunting skills of _C. galapagensis_. As no actual feeding behaviour of associated fish was observed on video footage, it is unclear whether large pelagic species attempt to strike prey detected by _C. galapagensis_ before the sharks, or whether they feed on injured individuals, or scavenge scraps from prey items taken by sharks.

Of the environmental variables measured in our study, water current speed had the greatest influence on the structure of pelagic fish assemblages. _Carcharhinus galapagensis, Seriola rivoliana_ and _Scomber australasicus_ were associated with lower flow environments, while _Seriola lalandi_ was associated with higher flow environments, although the range of current speeds recorded during the survey period indicated that the study area was characterized by relatively slow current speeds (0.03 to 0.34 m s\(^{-1}\); mean 0.17 m s\(^{-1}\)). Flow has previously been identified as an important aspect of habitat for fish assemblages on the SE Australian continental shelf (Williams & Bax 2001), and associations with particular flow conditions have been observed for other marine predators (Johnston 2005). Habitat preferences for particular flow conditions may relate to zooplankton dynamics—zooplankton are known to accumulate in island wakes, in areas of low flow (Suthers et al. 2004, 2006). Neither temperature nor depth influenced pelagic assemblages or abundances in our study. This result is contrary to previous studies (Freon & Misund 1999), but both variables had a very small range in our study (22.2 to 23.2°C temperature; 15 to 55 m depth).

### Estimating fish abundance from mid-water BRUV: accounting for current speed

Pelagic fish abundance can be best estimated from mid-water BRUV footage using MaxN/Plume (distance or area) rather than using MaxN/Attract (distance or area). The latter technique was developed by Sainte-Marie & Hargrave (1987) and Priede & Merrett (1996) for deep-sea BRUV studies, which generally have long soak times, on the order of days (e.g. Bozzano & Sardà 2002, Kemp et al. 2006), and which target organisms that are relatively slow moving (e.g. Collins et al. 1999b). In contrast, our mid-water BRUV surveys used a short soak time (45 min) and targeted fast-swimming species. Both these factors reduce the time between a fish’s detection of the bait plume and its subsequent appearance on video footage, minimizing the difference between plume size and distance or area of attraction. Our results are consistent with Ellis & DeMartini (1995), who conclude that deep-sea techniques for estimating abundance from video footage may not be suitable for BRUV studies conducted in shallower ecosystems.

We considered MaxN/Plume to provide more accurate estimates of pelagic fish abundance from mid-water BRUV, because MaxN/Attract requires additional data about fish swimming speeds, which is difficult to obtain (Lowe & Goldman 2001) and incorporates numerous, often untested, assumptions about fish behaviour around baits. For example, fish swimming speeds _around_ baited gears may not reflect swimming speeds _to_ the bait (Løkkeborg 1998, Kallayil et al. 2003). It is also unclear whether fish swim towards a bait at their natural or ‘foraging’ or ‘cruising’ speed, or at their maximum ‘burst’ speed—indeed the behaviour chosen may vary according to factors such as satiation or the degree of competition for food resources (Moore & Howarth 1996, Johansson & Leonardsson 1998). The strong link between fish swimming speed and body size (Plaut 2001, Krause et al. 2005) means that accurate estimates of swimming speed also require accurate estimates of fish size from BRUV footage, which are only possible through the use of stereo video (Harvey et al. 2003). The link between swimming speed and fish size is of particular concern where size varies systematically across treatments, e.g. among sample regions (e.g. Collins et al. 2005) or seasons (e.g. Smith et al. 1997).
Assumptions about bait dispersal proved important for the interpretation of our results. Using different plume models (MaxN versus MaxN/Plume$_{dua}$ versus MaxN/Plume$_{area}$) affected the outcome of regression analyses comparing fish assemblages and abundances with local current speeds. Significant correlations between pelagic fish assemblages and current speed and between Cararcharinus galapagensis abundance and current speed were only observed using MaxN/Plume$_{area}$. These different outcomes stem from the strength of the derived relationship between abundance indices and current speed. Plume$_{dua}$ increases linearly with current speed, while Plume$_{area}$ increases as a power function. These different outcomes demonstrate the difficulty in separating the dual effects of current speed in BRUV studies: the effect of current speed on bait dispersal and abundance estimates and the effect of current speed on fish abundance related to habitat preferences for particular flow conditions or correlated environmental variables (e.g. depth, temperature). These can only be resolved through more accurate current speed measurements and bait dispersion models. Modelling plume dynamics is a complex task, which would require separate dispersion models for each component of a bait mixture (e.g. oily components versus larger flesh or bread particles). In the absence of such models, we recommend that abundance be calculated from mid-water BRUV using an area-based estimate of plume dispersal, as this is a conservative estimate that is unlikely to generate falsely derived relationships. For studies with long soak times, bait plume area may be best approximated using an elliptical, rather than a triangular, area (Priede & Merrett 1996, Bailey & Priede 2002).

The importance of selecting an appropriate bait plume model is particularly evident when comparing fish assemblages or abundances across treatments, where current speed varies systematically among treatment groups, as observed for fished areas versus sanctuary zones at Lord Howe Island. Current speeds recorded in sanctuary zones around Lord Howe Island over our survey period were significantly higher than those recorded in fished areas (Fig. 7). Observed differences in flow between sanctuary zones and fished areas are likely to vary temporally with variations in EAC/Tasman Sea circulation patterns (Ridgway & Dunn 2003). MPA monitoring or other studies could be confounded if both regional and temporal variations in current speed are not taken into account. Our data on pelagic fish associations with particular flow conditions provides a standardized baseline for MPA monitoring, which allows any change in distribution or abundance following zoning to be assessed relative to the suitability of the surrounding habitat. The inclusion of current speed as a covariate when analyzing BRUV data can also account for these effects to some degree. We suggest that current speed should be measured using a drogue deployed simultaneously with each BRUV and for the duration of the BRUV as a Lagrangian measure of current that accounts for spatial and temporal variations in current speed or direction. Eulerian measures, like current meters and the short drogue deployment length used in this study, fail to account for small-scale spatial variations in current speed (e.g. eddies or gyres, topographically induced variations to flow; Suthers et al. 2004), which are likely to be as important as, or more important than, temporal changes in current speed for BRUV studies with short soak times (Sainte-Marie & Hargrave 1987, Hill & Wassenberg 1999, Henriques et al. 2002).

Consideration should be given to other cues that may attract pelagic fish to BRUVs. Sharks, including carcharhinds, can be attracted to low-frequency instrumental sounds, such as those emitted by a video camera, from a distance of up to 400 m (Myrberg 2001). Pelagic fish could also be attracted to BRUVs by the structure itself (Freon & Misund 1999) or by associated interruptions to surrounding currents (Popper & Carlson 1998). Even though we consider chemosensory cues to have been the most important in our study, knowledge of the ‘area of attraction’ for all relevant cues may enhance the accuracy of abundance estimates (e.g. Bailey & Priede 2002). Incorporating the ‘search area’ traversed by an actively foraging pelagic predator (e.g. Sainte-Marie & Hargrave 1987, Bailey & Priede 2002) may further enhance the accuracy of abundance estimates.

Our results do not represent a comprehensive comparison of fished areas and sanctuary zones in the Lord Howe Island Marine Park because of the small number of sites surveyed. Rather, they highlight the importance of accounting for current speed when mid-water BRUV is used to estimate fish abundance or to compare assemblages among regions or treatments with different flow conditions. Our results indicate that oceanographic characteristics can be important for pelagic fish habitat selection over the scale of kilometres, and these should therefore be considered during MPA zoning and monitoring. Surveys of the oceanographic characteristics of pelagic fish habitat around Lord Howe Island should be conducted over a longer time period and a broader scale of oceanographic influences (EAC, Tasman Sea) to identify priority areas for further research or conservation efforts for pelagic species.

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Food subsidies from fisheries to continental shelf benthic scavengers

Michel J. Kaiser*, Jan Geert Hiddink

School of Ocean Sciences, College of Natural Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

ABSTRACT: Fisheries generate carrion as a result of material discarded at sea from fishing boats, and as a result of the direct mortality of organisms on the seabed that is caused by the bottom trawling gears. It is unclear whether the increases in the population sizes in scavenging seabirds that have been partially attributed to discarding practices might be mirrored in populations of benthic scavengers. We used a previously published and field-validated, size-based model to calculate the effects of bottom fishing on benthic invertebrate production and production of invertebrate carrion at the seabed in the North Sea. This estimate was combined with previously published estimates of discarded fish carrion that reaches the seabed. Fishing decreases benthic biomass; this means that benthic production is also reduced. In this process, fishing increases production in the short term (2 to 3 d) by generating carrion. However, the production of carrion only compensates for 22% of the reduction in production. Calculations of ash free dry weight of carrion produced per unit area were similar to other previous estimates for the North Sea, which indicated that fisheries-generated carrion was sufficient to sustain benthic carnivores for only approximately 3 d yr⁻¹.

KEY WORDS: Benthic scavengers · Energy subsidies · Model · Fishing disturbance

INTRODUCTION

Food falls in the deep sea have important ecological implications for the patchiness of diversity in this environment (Stockton & DeLaca 1982), and may provide as much as 11% of the benthic community’s respiratory requirements (Smith 1985). Surprisingly, the ecological implications of these energy subsidies are less well studied for shallower continental shelf systems. This dichotomy has arisen, in part, due to the different approaches to sampling the faunal assemblage in these 2 environments: shallow continental shelf assemblages of mobile macrofauna are typically sampled with small towed trawls, whereas the mobile fauna of the deep sea are typically studied using baited underwater cameras (see papers in this theme section). These differences in approach have inevitably skewed our knowledge of deep-sea fauna towards those taxa that are attracted to carrion, whereas far less is known specifically about carrion-feeding taxa on the continental shelf. In addition, food falls and other sources of carrion that occur on the continental shelf, occur against a background of higher levels of primary production and natural and anthropogenic disturbances such that the effects of energy subsidies have been considered to be insignificant (Hall 1994). In addition to this, most circalittoral scavengers may be facultative rather than obligate scavengers (Britton & Morton 1994) and are unlikely to show the specialised morphological and life-history adaptations that are conducive to subsistence upon sporadic pulses of carrion (but see Kaiser & Moore 1999).

On a global scale, fisheries are a major source of carrion generated through discarded bycatches of organisms for which there is no market, for which fishers have no quota, or that are illegal to land. It is estimated that 27 million tonnes of such bycatch are discarded annually (Alverson et al. 1994). This figure is likely an underestimate, as it represents only reported bycatch and does not account for the inevitable increase in the proportion of discards as the biomass of legal-sized fishes diminishes further under a regime of continuing over-exploitation, although technological improvements in gear design have helped to reduce this prob-
problems (Hall & Mainprize 2005, Broadhurst et al. 2006). In addition to the material retained in fishing nets that is subsequently discarded, demersal trawls kill or damage varying proportions of different benthic taxa in the path of the trawl (Bergman & Van Santbrink 2000, Kaiser et al. 2006). The mean instantaneous mortality for different benthic taxa varies considerably (from 21 to 98%) according to their structural characteristics and position in the habitat (Table 1). Thus, fisheries generate considerable amounts of carrion, from both discards and incidental mortality on the seabed. This carrion acts as an energy subsidy to marine food webs by making available resources that would otherwise be unattainable for organisms at particular trophic levels.

Ecologists recognize the importance of resource subsidies from donor ecosystems and habitats to sustaining food webs in recipient ecosystems or habitats (Polis et al. 1997, Paetzold et al. 2005). In situations where food webs are subsidised, consumer populations can sometimes become enhanced (Polis et al. 1996), although this may depend on the quantity and temporal variability of the subsidy and on the life-history characteristics of the consumer species. Where consumers do increase in abundance as a result of food subsidies, several top-down effects may occur in the community. Subsidised consumers may depress in situ prey species; if these species are key to community structure, the effects could be far-reaching. When large numbers of subsidised predators depress herbi-vore populations, primary producers can become more abundant (Polis et al. 1996). For energy subsidies to have a population level effect, they must be sufficient in magnitude and frequency and must be predictable (Polis et al. 1996). On this basis, carrion generated through fisheries activities might be considered to have the potential to lead to population level changes in marine scavengers. The population level responses of avian scavengers to fisheries carrion is well documented, with changes in the population size of particular species that are predicated upon competitive capabilities and limitations imposed by foraging ability (Furness et al. 2007, this volume). These observations have prompted speculation that fisheries-generated carrion that reaches the seabed could lead to an increase in the population size of fish and benthic scavenger populations that can utilise fisheries carrion as a source of energy (Link & Almeida 2002). The purpose of the present paper was to examine the evidence for the latter supposition by reviewing briefly what we understand about scavenger behaviour in relation to fisheries carrion. We then examine through a modelling approach whether the inputs of carrion are likely to meet the criteria defined by Polis et al. (1996).

Responses of scavengers to fisheries carrion

Direct observational studies of the response of marine aquatic scavengers to fisheries discards are limited and have been undertaken primarily in northern Europe and Australia, with a few studies undertaken in North America and the Mediterranean. These studies are divided into 3 main categories: (1) laboratory observations of different scavenging taxa consuming discarded material from fisheries, (2) analysis of the diets of scavengers in areas subjected to fishing disturbance compared with appropriate control conditions, and (3) direct quantification of scavengers using baited traps or video cameras.

Although the species that consume fisheries discards differ between studies undertaken in the northern and southern hemisphere, the groups of scavengers were broadly similar, e.g. seabirds (Furness et al. 2007), fishes, crustaceans and gastropods. The composition of scavenger assemblages may vary considerably with habitat type (Ramsay et al. 1997). The outcome of interactions over carrion may be related to competitive ability that is also influenced by the background density of a particular species (Ramsay et al. 1997). Accordingly, the responses of different scavenger species to increasing inputs of carrion may vary between habitats, and we might expect to see different population-level responses at a habitat scale that is smaller than the scale applying to scavenging seabirds (Furness et al. 2007).

<table>
<thead>
<tr>
<th>Gear type and habitat</th>
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<th>Mean Day 1 change (%)</th>
</tr>
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<td></td>
</tr>
<tr>
<td>Gravel</td>
<td>Ann, Cru, Ech, Moll</td>
<td>–42</td>
</tr>
<tr>
<td>Sand</td>
<td>Ann</td>
<td>–21</td>
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<tr>
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<td>Ann, Cru, Ech, Moll</td>
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<tr>
<td>Oth</td>
<td>Oth</td>
<td>–54</td>
</tr>
<tr>
<td>Otter trawls</td>
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</tr>
<tr>
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<td>CnP</td>
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<tr>
<td></td>
<td>Moll</td>
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<tr>
<td></td>
<td>Ech, Oth</td>
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<td></td>
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Table 1. Mean instantaneous percentage mortality (up to 1 d after initial fishing gear impact) of different Phyla grouped by fishing gear type (beam or otter trawls) and habitat (gravel, sand, muddy sand, mud and biogenic). Phylum—Ann: Annelida, Cru: Crustacea, Moll: Mollusca, Ech: Echinodermata, CnP: Cnidaria and Porifera, Oth: Other Phyla. Data adapted from Kaiser et al. (2006).
Laboratory observations

Berghahn (1990) studied benthic scavenger feeding on discarded fish from shrimp trawl fisheries in the shallow waters of the Wadden Sea, and found that the shrimps *Crangon crangon*, the crabs *Liocarcinus depurator* Fabricius and *Carcinus maenas*, the starfish *Asterias rubens* and the whelks *Buccinum undatum* L. feed on freshly killed discards presented in the laboratory. Berghahn (1990) also calculated the food intake rates for *C. maenas* and *C. crangon*, and found that these were 0.40 to 1.33 and 0.034 to 0.093 g wet wt specimen⁻¹ d⁻¹, respectively. Interestingly, Berghahn (1990) also noted that shrimps were unable to consume the flesh of the fish until it had begun to degrade (after 24 h). In a similar study, Evans et al. (1993) examined the response and consumption of whelks to 3 different discard taxa in laboratory choice experiments. Whelks ate swimming crabs *Liocarcinus depurator*, purple heart urchins *Spatangus purpureus* and a gadoid fish, the pouting *Trisopterus minutus*, but not plaice *Pleuronectes platessa*. Whelks moved most rapidly towards swimming crabs, suggesting that these were the most preferred prey type. Although the rate of energy intake was highest when whelks fed on sea urchins, when fed to satiation they acquired most energy from swimming crabs. When presented with whole animals, whelks fed preferentially on specific body tissues, e.g. they consumed the eyes of pouting first, and never ate the gills or carapace of swimming crabs. Absorption efficiency was highest when fed a diet of swimming crabs (93%) and lowest when fed pouting (83%). These experiments revealed that whelks preferentially consumed the most energetically rich species. These laboratory observations were later validated with trapping experiments using different types of carrion (Ramsay et al. 1997).

These laboratory observations reveal some useful insights into a number of aspects of the use of carrion by scavengers in the field. Firstly, it is clear that many species of scavengers are capable of feeding upon the same types of carrion (e.g. fish), but that some scavengers such as whelks show distinct preferences for particular types of carrion (e.g. swimming crabs) that yield the most energy. Other carrion types are avoided, presumably because they are unable to physically utilise them or for other reasons such as aversion to the tissues of particular species (e.g. plaice). These combined observations suggest that competition and resource partitioning are likely to occur with respect to dead discards that fall to the seabed and moribund animals generated by the direct physical disturbance created by the trawl.

In situ observations

The limitation of laboratory studies of putative scavenging species is that the observations may not relate to what happens in the field. A number of studies have approached this through direct observation of scavengers attracted to underwater time-lapse still or video cameras baited with moribund discards, through direct time-series observations using divers, or through experimental manipulations in the field and remote sampling. Each of these approaches has offered complimentary information regarding the behaviour of scavengers in the field. Kaiser & Spencer (1996) recorded the numbers of scavengers feeding on a bag containing bait at a site in the Irish Sea, and found that the main scavengers were dabs *Limanda limanda* L., whiting *Merlangius merlangus* L., hermit crabs *Pagurus bernhardus* L., whelks *Buccinum undatum* and starfish *Asterias rubens*. Similar studies have been carried out in Australia in Moreton Bay, Queensland, and the Torres Strait between Australia and Papua New Guinea (Hill & Wassenberg 1990, Wassenberg & Hill 1990). In the Moreton Bay prawn fishery, those discards that reached the sea bed were eaten by sand crabs *Portunus pelagicus* L. and fish (Wassenberg & Hill 1990). Most of the material from the Torres Strait prawn fishery that reached the sea bed was eaten by teleost fish and sharks (Hill & Wassenburg 1990). These time-lapse camera observations yield useful insights into arrival times and residence time at food falls. Kaiser & Spencer (1996) found that the arrival times at fisheries carrion varied according to scavenger mobility. The most mobile scavengers such as dabs, whiting and hermit crabs arrived between 30 and 50 min after deployment of the carrion, while slower-moving scavengers built up in numbers more slowly, with whelks arriving after 7 h. Similarly, peak numbers of different species occurred at different times after the initial food fall, with maximum hermit crab densities at 3 to 14 h, whelks at 12 h and starfish at 17 h or longer. In another related study, Ramsay et al. (1997) undertook similar observations at 2 sites within the Irish Sea, one at a site with a muddy sand substratum and the other at a site with a muddy substratum. Observations with baited time-lapse cameras at the muddy sand site showed that the hermit crab *P. bernhardus* was attracted to carrion in greatest abundance and aggregated at densities of up to 330 m⁻², and there was a much greater diversity of scavengers at this site. In contrast, there was relatively little scavenging activity at the muddy substratum site, where the edible crab *Cancer pagurus* appeared to consume the greatest proportion of the carrion. Numbers of each scavenger species at the bait were only partially related to the background population density of each species at each
site; hence, the differences in attraction to the carrion are probably related to the seabed water current speed at these sites (high at the muddy sand site, low at the muddy site). As a consequence of the different numbers of scavengers attracted to the carrion, the rate of consumption of carrion varied between sites and could be related to the abundance of different scavenger species at the bait.

The numbers of scavengers attracted to fisheries carrion varies among different habitats. In those habitats where scavenger numbers are high and high densities of scavenger aggregate around carrion, there is ample evidence of competition within and among species (Ramsay et al. 1997, Kaiser et al. 1998). Evidence for the latter was particularly apparent for hermit crabs Pagurus bernhardus and Pagurus prideaux in the Irish Sea. Both of these species are attracted to and consume carrion in laboratory studies. However, direct field observations demonstrate that P. prideaux avoid carrion when large aggregations of P. bernhardus occur and that the latter also exclude, through competitive interactions, the smallest individuals in the population.

The consumption time for carrion on the seabed has been ascertained in a number of in situ studies, and varies from 3 to 72 h (Berghahn 1990, Ramsay et al. 1997, Fonds & Groenwold 2000, Groenwold & Fonds 2000). While these consumption times reflect the number of scavengers attracted to the carrion, they are also similar to the time-scale at which scavenger aggregations persist on trawled areas. The latter have been ascertained through comparative studies of experimentally trawled areas with suitable adjacent control areas sampled at times before and after trawl disturbance occurred. All such studies indicate that the abundance of a variety of scavengers increases within trawl-disturbed areas relative to control areas up to 72 h after the trawl disturbance occurred and thereafter declines (Kaiser & Spencer 1996, Ramsay et al. 1996, Kaiser et al. 1998, Demestre et al. 2000). This time-scale approximates well the arrival behaviour and patterns of scavengers at baited cameras. Scavenging fauna sampled from within trawl-disturbed areas typically have fuller guts than those sampled from adjacent untrawled areas (Kaiser & Spencer 1994, Ramsay et al. 1996), and even contain species of carrion that would not be available to them under normal conditions (Kaiser & Spencer 1994, Link & Almeida 2002).

How much carrion is produced and where does it go?

In the North Sea it has been suggested that the total weight of fish discarded annually is in the same order of magnitude as the total landings of the demersal fisheries (Camphuysen et al. 1993). The total annual quantity of discards and offal in the North Sea has been estimated at 70 000 tonnes of offal, 120 000 tonnes of roundfish, 200 000 tonnes of flatfish and 180 000 tonnes of benthic invertebrates (Camphuysen et al. 1993). The mortality of discards varies between different species; some fish such as dragonets Callionymus lyra L. are extremely vulnerable, nearly 100% die after capture, whilst others, such as the starfish Asterias rubens L., are less susceptible to physical damage and <1% die (Kaiser & Spencer 1995). Nevertheless, there is significant bias introduced into studies that examine post-trawl survival in the absence of natural predators, which can lead to greatly under-estimated mortality rates (Ramsay & Kaiser 1998). A large proportion of the discarded non-commercial or undersized fish is eaten by seabirds (Furness et al. 1988, Camphuysen et al. 1993), the number taken varying according to the species discarded, as most seabirds eat roundfish in preference to flatfish (Furness 1996, 2003, Furness et al. 2007). It has been suggested that increases in the population sizes of some scavenging seabirds can be linked (in part) to increased food availability in the form of fisheries discards (Furness et al. 1988). Those discards not eaten by seabirds will sink through the water column where some may be eaten by cetaceans and fishes (Hill & Wassenburg 1990); the remainder sink to the sea bed where they become available as food for benthic scavengers. In the North Sea, it is considered that approximately half of the discarded material from trawlers sinks to the seabed, but this varies from one region to another (Garthe et al. 1996, Furness et al. 2007).

Although the amount of organic material redirected to the seabed may seem large (>300 000 t), there is a further source of carrion generated in the path of the trawl through direct physical disturbance. The latter can generate considerable amounts of carrion that varies with gear type and the habitat in which it is employed (Kaiser et al. 2006). Incorporating this additional source of mortality is important if we are to understand the ecological implications of fisheries-generated carrion for the scavenging biota of benthic communities (Fonds & Groenwold 2000).

Trends in the abundance of benthic scavengers

A number of studies have used long-term datasets to gain an insight into potential changes in scavenger populations. However, Philippart (1998) found no increase in the reported numbers or frequency of landings of scavenger species by Dutch fishermen; indeed, some species such as common whelk Buccinum undatum had become locally extinct. In contrast, Rumohr &
Kujawski (2000) compared qualitative historical benthos data (1902 to 1912) with recent data (1986) and found long-term trends in epifauna species composition in the southern North Sea that they attributed to fishery-induced changes. Scavenger and predator species (crustaceans, gastropods and sea stars) were observed more frequently in 1986. There was a marked increase in records of starfish, and the frequency of occurrence of the common whelk had more than doubled. The swimming crab *Liocarcinus holstus* also increased markedly Rumohr & Kujawski (2000). Greenstreet & Hall (1996) also reported that the abundance of scavenging flatfish such as dab had also increased during the last century. Although such studies are useful in detecting long-term trends in scavengers, these changes are likely also linked to fisheries-induced reductions in competing species and top predators such as cod, as well as long-term changes in the environment.

**MATERIALS AND METHODS**

Demersal fisheries kill benthic invertebrates as the fishing gear is dragged across the seabed and generate carrion through discarding of bycatches. These killed animals and carrion contribute to secondary production of animals that feed on this material and therefore can cause a short-term increase in local production. Nevertheless, previous studies have shown that chronic bottom trawling reduces the overall biomass and production of benthic invertebrate communities due to the removal of the large biomass of large and long-lived fauna (Hiddink et al. 2006b). Here, we partition out the energy subsidy generated through fisheries activities to estimate its importance for marine carnivores.

Modelling benthic production and carrion production. We used an existing size-based model to calculate the amount of benthic production and production of benthic carrion that occurs in the North Sea under a quantified regime of different intensities of trawling disturbance. Details of the development and use of the model are given in Duplisea et al. (2002) and Hiddink et al. (2006b). In brief, the model contained 32 state variables, in 2 faunal groups (soft- and hard-bodied macrofauna). Growth of the population biomass in each body mass–organism type compartment was modelled by modifying Lotka-Volterra competition equations to give the population biomass flux for a compartment. The size-based approach of the model is advantageous because it can be applied to a wide range of environments for which the physical forcing parameters are known. The interaction between habitat type and trawling effects was modelled by including relationships between growth, mortality and the environment in the model. Thus, sediment type affected trawling mortality, sediment erosion rates affected natural mortality, the effect of bed shear stress modified population growth rate and the chlorophyll a content of the sediment affected carrying capacity. The interaction of organisms with the environment is independent of body type and depends solely on their life-history parameters. As soft- and hard-bodied invertebrates have different life-history parameters in the model, at the same body size, soft-bodied animals have a faster life history than hard-bodied animals; therefore, hard-bodied animals dominate stable habitats and soft-bodied animals prevail in the more dynamic and disturbed habitats. The model was validated by correlating observed and predicted values of biomass at each of 33 stations that were subject to a known range of trawling intensities in 4 shallow, soft-sediment areas in the North Sea. The sources of environmental data used to parameterise the model and the sensitivities of the model to changes in parameters were described by Hiddink et al. (2006b). We recalculated the model predictions from ash free dry weight (AFDW) to wet weight (Wet wt) using a conversion factor of 6.73 (Brey 2001).

In the original model, production was the sum of carrion and ‘normal’ production. Carrion production in the model was calculated separately for animals larger and smaller than 0.5 g as the biomass of animals that were killed by trawling in a year. The ‘normal’ production is defined as the biomass of all animals that die in a year excluding carrion production. The model was used to examine the effect of bottom trawling on benthic production in the Dutch and UK sectors of the North Sea (125 000 km²), in the area south of 56° N for 9 km² cells. Production and biomass in the presence and absence of trawling were determined by running the model for 1500 time steps of 30 d. The general effect of trawling on production is illustrated for 2 habitats with different sensitivities to bottom trawling. Sensitivity $S$ was defined based on the time it takes for production to recover to 90% of its pristine values (as calculated with the size-based model described by Hiddink et al. 2006a, 2007):

$$S_p = 1 - e^{-0.25T_p}$$

where $T_p$ is the time that it takes the productivity of the benthic community to recover from the trawling impact.

Trawling frequency was calculated from European Community Satellite Vessel Monitoring System (VMS) data (for more details see Dinmore et al. 2003, Hiddink et al. 2006b). For the Dutch beam-trawling fleet, VMS records were not available for all vessels. Therefore, effort distribution, as recorded by the VMS system,
was corrected to represent total trawling effort as recorded in logbooks by fishers (G. J. Piet, RIVO, unpubl. data). To express trawling frequency, the North Sea was gridded at a scale of 9 km² and trawling intensity was expressed as the number of times each 9 km² grid cell was swept each year. In this calculation it was assumed that trawlers fished at a speed of 5 knots, with a total fishing gear width of 24 m (2 beam trawls each of 12 m width or 1 otter trawl of 24 m width). Therefore, at a VMS record frequency of once per 2 h, 1 satellite monitoring record in 1 grid cell represents a trawled area of 0.449 km² and 1 record in 1 grid cell in a 1 yr period represents a trawling intensity of 0.050 yr⁻¹.

**Calculation of carrion from discards.** In addition to the carrion generated directly through bottom trawl disturbance, we calculated the amount of carrion generated through discarding, using the values reported by Garthe et al. (1996). In their study, Garthe et al. (1996) calculated the different amounts of fisheries discards generated by trawl fisheries in different spatial areas of the North Sea and estimated the amount of this material consumed by scavenging seabirds from direct observations of the feeding behaviour of seabirds while at sea. Our model extended to 125 000 km² of the North Sea and covered 40% of the central west, 49% of the central and 60% of the southern areas of the North Sea, as defined by Garthe et al. (1996), and discard estimates were scaled to the modelled area. For each of these areas, we calculated the proportion of discards that were not consumed by seabirds and used these to correct for the actual weights of discarded material. In the original calculations by Garthe et al. (1996), they reported separately the benthic invertebrate component of discards; however, this component is already accounted for in our estimate of instantaneous mortality in the benthos as a result of trawling (i.e. the difference in the benthos observed before and after a trawling event includes the benthos killed on the seafloor and that retained within the trawl net and subsequently discarded).

**RESULTS**

The mean instantaneous mortality varied among taxa, with different gear types (otter trawls vs. beam trawls) and among habitats (Table 1). Knowing the difference in the instantaneous mortality of benthos with gear type and habitat enabled us to integrate these differences through modelling. Accordingly, we calculated the change in benthic production for different body-sized animals in response to different intensities of trawling in the North Sea. We showed only the output for the most sensitive seabed habitat ($S = 0.8$ to $1.0$) and the second least sensitive seabed habitat ($S = 0.2$ to $0.4$) for illustrative purposes. The latter covered 42.6% of the area of the North Sea considered in the present study (Tables 2 & 3, Fig. 1). The output for both habitat types indicates that the production of benthic carrion is trivial compared with total benthic production, even when overall benthic production is reduced by the direct effects of trawling disturbance. As reported previously, the smaller body-sized components of the fauna ($<0.5$ g) increase their production under a regime of irregular fishing disturbance (disturbed once every 0.25 to 4 times yr⁻¹ (Fig. 2). It is clear from the satellite monitoring data that most areas of the seabed are trawled relatively infrequently, while others are trawled intensively. Interestingly, the response of the production of carrion is quadratic, as reported elsewhere (Ramsay et al. 2000), such that the production of carrion increases under intermediate regimes of disturbance and then declines again as fishing frequency increases above 2 to 4 times yr⁻¹ depending on the habitat sensitivity.

Using the corrected values (see Table 2 legend) given in Garthe et al. (1996), we calculated that excluding benthic discards, the total amount of material recycled to the seabed (roundfish, flatfish, elasmobranchs and offal) for the central west, central and...
southern regions of the North Sea amounted to 117 173 t yr\(^{-1}\). Our modelled estimate of total benthic carrion produced by the direct physical disturbance created by trawling at the seabed was 255 783 t yr\(^{-1}\) (Table 3). This sums to give a total production of carrion made available to benthic scavengers of 372 956 t yr\(^{-1}\) compared with a total benthic production under the current regime of fishing disturbance of 5 185 369 t yr\(^{-1}\), excluding the contribution of carrion. This also ignores the contribution of those organisms that pass through the meshes of the net, but that subsequently die. The loss of production from trawling due to biomass removal (excluding the contribution of carrion) equates to 1 702 165 t yr\(^{-1}\). This means that carrion generated by direct physical disturbance to the seabed is equivalent to only 15% of the benthic production that is lost due to trawling. Adding the contribution of carrion from discards increases the biomass of carrion to 22% of the loss of production in the benthos due to trawling. Garthe et al. (1996) estimated that the amount of benthic material discarded to the seabed in the area considered in the present study was 54 970 t yr\(^{-1}\). The latter represents only 21% of our modelled estimate of carrion production (255 783 t yr\(^{-1}\)) that takes into account mortality on the seabed (Table 3).

**DISCUSSION**

Increases in the populations of avian scavengers in the North Sea and elsewhere have been linked, in part, to the activities associated with discarding practices from fisheries. However, to date, no similar increases in benthic scavengers have been recorded for either invertebrates or fishes (Ramsay et al. 2000). Nevertheless, scavenger species may become the dominant macrofauna in areas subjected to intensive bottom fishing activities without changing their abundance (i.e. other species are simply removed, while scavenger populations do not change). Fonds & Groenwold (2000) used an energetic approach to calculate the energy requirements of benthic carnivores relative to the amount of carrion generated through fishing activities for 4 study areas in the North Sea. They calculated that the fisheries in this region generated 1.27 g AFDW m\(^{-2}\) yr\(^{-1}\), which was approximately enough to sustain benthic carnivores for 10 d given maximum consumption rates at 16°C. Converting the combined estimates of wet weight of carrion produced to AFDW using a conversion factor of 6.73, Brey (2001) gives a value of 0.556 g AFDW m\(^{-2}\) yr\(^{-1}\) for the area of the North Sea considered in the present study. These 2 independent estimates are similar in terms of magni-
tude, and we would reiterate the conclusions of Fonds & Groenwold (2000) that there is likely insufficient carrion generated by fishing activities to stimulate an increase in the populations of these taxa at a North Sea-wide scale. A supply of carrion that can sustain scavengers for 10 d represents an increase in yearly food supply of 2.7%, suggesting that this would lead to a proportionate increase in the abundance of scavengers. Most scavengers in the North Sea are facultative and rely on food resources other than carrion. However, chronic bottom trawling not only produces carrion, but it also substantially reduces the production of the remaining benthic community, which forms the natural food source consumed by facultative scavengers. In the North Sea, benthic invertebrate production is reduced by 21% compared to a situation without bottom trawling (Hiddink et al. 2006b), and this means that fisheries are likely to reduce rather than increase food availability for scavengers.

Given the variation in fishing disturbance frequency across the North Sea it is possible to consider that in some areas conditions may exist that would promote scavenger populations. A cursory examination of Fig. 2 might indicate that, at the lower levels of fishing frequency, carrion does offset losses of production due to fishing; however, occurrences are so infrequent (every 4 to 8 yr) that they clearly do not meet the criteria defined by Polis et al. (1996): if energy subsidies are to have population level effects, they must be large enough and occur frequently and in a predictable manner. These criteria are met for avian scavengers, as they are able to search widely for (and find) trawlers on a daily basis and thereby remove the unpredictability of the supply of discards.

Despite our conclusions, carrion generated from pelagic fisheries may have a positive population effect on scavengers. Pelagic fisheries do not interact with the seabed; hence, there is no net loss of benthic biomass or production due to interactions with the gear. Assuming that most roundfish discards originate from pelagic fisheries and that the other sources of discards originate from demersal fisheries (Table 2), pelagic fisheries contribute ~11% of total discard flux to the seabed. This implies that discards of pelagic fisheries in areas where there is no bottom trawling could have a significant effect on benthic scavenger populations. We hypothesize that scavengers may be more abundant in areas that are exploited exclusively by pelagic fisheries compared to areas where bottom-trawl fisheries occur. This prediction could be tested by combining detailed fishing effort distribution data with sampling of benthic invertebrate communities. Given the variation in pelagic fishing frequency across the North Sea, it is possible to consider that the latter conditions occur in some areas (Greenstreet et al. 1999).

Secondary effects of fishing may also have an impact upon benthic scavenger populations that create bottlenecks to population growth. Many of the benthic scavengers considered in previous studies are themselves subject to fisheries mortality, which is often underestimated in controlled laboratory survival experiments (e.g. Berghahn 1990, Kaiser & Spencer 1995). Examination of post-fishing mortality in natural conditions revealed that whelks were extremely susceptible to predation by hermit crabs and starfish compared with whelks that were unaffected by contact with a fishing gear (Ramsay & Kaiser 1998). Fishing may also affect the availability of essential resources such as gastro-
pod shells for hermit crabs. In a comparative study of the North and Irish Seas, Kaiser et al. (2002) found evidence that hermit crabs in the North Sea were smaller in body size in accordance with a lower availability of suitable gastropod shells due to the decline in whelk populations. Finally, most benthic scavengers on continental shelves are facultative scavengers whose morphology and physiology are not adapted to feeding on sporadic food falls and gorge feeding. However, amphipod scavengers fulfil these criteria, and are highly abundant at food falls in the North and Irish Seas (Ramsay et al. 1997, Groenwold & Fonds 2000). This group remains relatively little studied in terms of their population dynamics, but they would currently seem the most likely candidates to benefit from the carrion generated by fisheries as their life histories are adapted to infrequent pulses of food to the seabed. In an evolutionary context, amphipod scavengers would seem the only invertebrates that have evolved to cope with sporadic food falls. It is unlikely that such evolutionary adaptations could occur in other groups over the time-scale of the increase in commercial fisheries (last 40 yr). From an energetic perspective, it seems feasible that some fish could exist exclusively as scavengers (Ruxton & Huston 2004), but no evidence appears that would support this for large macro-invertebrates (Fonds & Groenwold 2000).

Although our modelling approach produces estimates of the amount of carrion generated through trawling, the figures derived are similar to those of other researchers whose calculations were based on empirical observations (e.g. Berghahn 1990, Fonds & Groenwold 2000). While food falls of carrion would not appear to offset the loss in total production attributed to the direct effects of fishing, the response of scavengers in the deep-sea environment may be quite different. With the expansion of commercial fisheries into ever deeper environments, the role of fisheries-generated carrion in deep-sea food webs warrants further investigation. Fisheries-generated carrion in the deep sea may well lead to population changes in a large range of scavenging species that are specifically adapted to exploit sporadic food falls, and Ruxton & Houston (2004) have demonstrated already the energetic feasibility of an obligate scavenging lifestyle for large-bodied fishes.

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Spatial and temporal variation in reef fish assemblages of marine parks in New South Wales, Australia—baited video observations

Hamish A. Malcolm¹,⁵*, William Gladstone², Steven Lindfield², James Wraith³, Tim P. Lynch⁴

¹Solitary Islands Marine Park, NSW Marine Parks Authority, PO Box J297 Coffs Harbour Jetty, New South Wales 2450, Australia
²School of Environmental and Life Sciences, University of Newcastle (Ourimbah Campus), PO Box 127, Ourimbah, New South Wales 2258, Australia
³School of Biological Sciences, University of Wollongong, Northfields Ave., Wollongong, New South Wales 2522, Australia
⁴Jervis Bay Marine Park, PO Box 89, Huskisson, New South Wales 2540, Australia
⁵National Marine Science Centre, University of New England, PO Box J321 Coffs Harbour Jetty, New South Wales 2450, Australia

ABSTRACT: Baited remote underwater video stations (BRUVS) were used to examine variation in assemblages of reef fishes at scales of 100s of kilometres (between 3 marine parks in New South Wales, Australia) and kilometres (between 4 sites within each park). Temporal variation over 5 yr was also examined in 1 park (Solitary Islands). BRUVS were able to sample the relative abundance and distribution of species from a wide range of trophic groups, and were particularly effective for detecting cryptic predators. Significant variability in the fish assemblages occurred between each park consistent with the latitudinal distribution of the parks. Fish assemblages also varied significantly between sites within each park. Contrary to expectations, total species richness did not follow the expected latitudinal gradient. However, observed geographical patterns in species richness of certain families such as Labridae (greater richness in the most northern park) and Monacanthidae (greater species richness in southern parks) followed expectations. Abundant schooling species, common to all 3 parks, were important contributors to variation between sites. Temporal variation over 5 yr at 1 park was relatively minor compared to the spatial variation among the 3 parks. This suggests large-scale spatial separation is more important for structuring fish assemblages than time. A network of marine parks will therefore be required to represent variation in reef fish assemblages over this latitudinal scale.

KEY WORDS: Baited remote underwater video stations · BRUVS · Marine protected area · Reef fish assemblage · Representativeness · Spatial patterns

INTRODUCTION

Reef fishes are an important component of marine biodiversity and include species that provide both top-down control of reef ecosystems through trophic cascades (Babcock et al. 1999) and the biomass of recreational and commercial fisheries (Henry & Lyle 2003). Understanding the distribution of reef fish assemblages at a range of spatial scales is a critical step towards identifying important underlying ecological factors and processes (Underwood et al. 2000). This knowledge is also necessary for the selection and design of marine protected areas (MPAs) that aim to be comprehensive, adequate and representative (CAR) in their conservation of reef fishes (Lubchenco et al. 2003, Gladstone 2007).

Application of the CAR principles relies on suitable data being available on the distribution and abundance of biodiversity. However, the majority of our understanding of spatial variation in reef fish assemblages is based on either diver-based underwater
visual census (UVC) surveys in shallow water (<15 m) (Barrett 1995, Edgar & Barrett 1999, Anderson & Millar 2004) or capture methods such as trapping (Cappo & Brown 1996). The relative paucity of studies at depths >15 m is a result of logistical constraints (such as those associated with no-decompression diving limits), selective constraints due to fishing gear biases, or sampling constraints such as topographically complex environments that make trawl sampling impractical.

The use of baited remote underwater video stations (BRUVS) (Cappo et al. 2003, 2004) provides a logistically feasible alternative or complementary method to UVC that can be used at various depths and in topographically complex habitats. Similar to sampling methods used to capture reef fishes, such as angling and trapping, BRUVS are biased toward species attracted to baits (Willis et al. 2000). However, this bias may be advantageous for conservation and fisheries management purposes as it provides information on species that are targeted or caught as by-catch with baits. In particular, BRUVS are able to detect rarer large predatory fish and shy cryptic species with less sampling effort than diver transects or unbaited video stations (Watson et al. 2005). Baited video techniques have been successfully used for a variety of applications along the continental shelf, such as monitoring the recovery of fishes in MPAs (Westera et al. 2003, Willis et al. 2003), indexing abundance of commercially important juvenile fish compared to long line catch per unit effort (Ellis & DeMartini 1995), comparing fish assemblages over large spatial scales (Stobart et al. 2007) and as a non-destructive alternative for describing spatial groupings of fish assemblages on commercial trawl grounds (Cappo et al. 2004). The non-destructive nature of BRUVS is especially important for studies located in MPAs, where conservation is the priority.

Conservation planning in MPAs occurs at a hierarchy of nested spatial scales (Margules & Pressey 2000, Ferrier 2002). For example, the selection of several large MPAs that aim to conserve biodiversity across several bioregions requires information at a spatial scale of 100s of kilometres. The zoning of individual multiple-use MPAs (e.g. into areas where extraction is allowed or prohibited) requires biodiversity data at scales of kilometres to 10s of kilometres, or smaller (ANZECC TFMPA 1998). Given their previously mentioned advantages, BRUVS have significant potential as a sampling technique to compare reef fish assemblages for conservation planning at multiple scales. However, comparing samples from single points in time can potentially lead to erroneous conclusions due to differences associated with temporal variability (Stobart et al. 2007). The stability of assemblage patterns over years has not been reported in previous BRUVS studies in the literature and therefore requires examination.

The broad aim of the present study was to compare reef fish assemblages using BRUVS below depths suitable for UVC methods, at scales useful to marine park planning, and to examine the potential for these patterns to persist over years. The specific objectives were: (1) to assess the assemblage of scavengers and other species of reef fishes sampled by this technique on rocky reefs in depths of 15 to 30 m, (2) to describe the spatial structure of reef fish assemblages by comparing reef fish assemblages between 3 marine parks (separated by 100s of kilometres) and between sites within each park (separated by kilometres), and (3) to test the temporal stability of fish assemblages over 5 yr at 1 marine park using these methods.

In New South Wales (NSW), on the eastern coast of Australia, a network of MPAs has been established across 3 of the 5 bioregions that span the NSW coastline (NSW Marine Parks Authority 2006). Given that bioregions delineate areas with different ecological characteristics (ANZECC TFMPA 1999), differences in reef fish assemblages between marine parks were expected at this scale. We also expected that species richness of fishes would decline southward given the latitudinal gradient of Australia’s east coast (Jablonski & Sepkoski 1996).

**MATERIALS AND METHODS**

**Study areas and sampling design.** Six large multiple-use marine parks have been established as part of a network of MPAs in NSW. This includes Solitary Islands Marine Park (SIMP), Port Stephens-Great Lakes Marine Park (PSGLMP) and Jervis Bay Marine Park (JBMP), which are spaced over 5° of latitude (Fig. 1). Each of these marine parks is separated by at least 300 km and is judged to be in a different bioregion (ANZECC TFMPA 1999).

Sampling occurred in these 3 marine parks, at 4 sites within each park that were separated by 2 to 20 km (Fig. 1). Eight replicate BRUVS were set in each site (i.e. n = 32 replicates park⁻¹). Within each site we haphazardly sampled rocky reef in depths of 15 to 30 m. Multiple (3 or 4) BRUVS were deployed within 5 to 10 min of each other. With limited knowledge of the response of a broad suite of species to a bait plume, a minimum distance of 200 m was kept between replicates to attempt to maintain a level of independence. Each video was deployed for 30 min, and only those with a full field of view were retained for analysis. Colour depth sounders were used to select reef habitat in the required depth range, and the distances between replicates were determined with global positioning systems (GPS). The JBMP sites were sampled in 2005; PSGLMP, in 2006; and SIMP sites, in 2002 to 2006. Sam-
dancing. This field of view represents a volume of 9.4 m^3 of water visibility on our measure of relative abundance (M. Coram & W. Gladstone unpubl. data). As the counts reflect relative abundance and not density, the data were expected to be robust to variability between observers in estimating this field of view.

Analysis of video-tapes. Video-tapes were reviewed on a standard television screen connected to a video camera. The identity of each fish species and an index of its relative abundance (MaxN) were recorded. MaxN was the maximum number of individual fish of each species in the frame at any 1 time during the 30 min video record. This eliminated the chance of recounting the same fish. Species accumulation curves for each park were used to determine sampling adequacy (EstimateS software, Colwell 2005).

Multivariate analyses. Non-metric multidimensional scaling (nMDS) ordination, based on a Bray-Curtis dissimilarity matrix of fourth-root transformed data, was used to visually depict variation in assemblage structure (Clarke 1993) (PRIMER software, Plymouth Marine Laboratories). Centroids of the assemblage at each site were displayed on the nMDS ordination because of the large number of replicate samples (Anderson 2001), and determined using PCO software (Anderson 2003). Distance-based permutational multivariate analysis of variance (PERMANOVA) was used to test the null hypothesis of no difference in assemblage structure between parks and between sites nested within parks using PERMANOVA software (Anderson 2005). The factor Park was analysed as an orthogonal, fixed factor with 3 levels (SIMP, PSGLMP, JBMP), while the factor Site was analysed as a random factor with 4 levels nested in each park. The PERMANOVA test for differences in assemblage structure between years and sites in SIMP treated years as an orthogonal, fixed factor with 5 levels (2002 to 2006) and sites as a random factor with 4 levels.

Species responsible for dissimilarity in the assemblage structure of fishes were determined with the similarity percentages routine (SIMPER) in PRIMER. We considered that large values (i.e. >1) of the ratio of δ_i/SD(δ_i) for a species (where δ_i is the average contribution of the i-th species to the overall dissimilarity [δ] between 2 groups and SD is standard deviation) indicated the species was consistently important to dissimilarity in all pairwise comparisons of samples in 2 groups (Clarke 1993). We considered species with %δ_i > 3% and with δ_i/SD(δ_i) > 1 as being important contributors to dissimilarity between parks (Terlizzi et al. 2005).

Univariate analyses. The null hypothesis of no difference in abundance between parks and between sites (parks) was tested with 2-factor analysis of variance (ANOVA) (GMAV software, Institute of Marine Ecology, University of Sydney). The variables tested were relative abundance (mean MaxN) for those species determined by SIMPER analysis as being important contributors to differences between parks in assemblage structure. Prior to ANOVA analysis, the assumption of homogeneity of variance was tested by Cochran’s test (Underwood 1981). Where necessary, data were ln(x+1) transformed to homogenise variances. When this transformation was unsuccessful, the raw data were analysed, as ANOVA is robust to depar-

Fig. 1. Marine parks in New South Wales (NSW), Australia, showing sampling sites (1 to 4) at the Solitary Islands Marine Park (SIMP), Port Stephens-Great Lakes Marine Park (PSGLMP) and Jervis Bay Marine Park (JBMP). Other marine parks in NSW are: Cape Byron Marine Park (CBMP), Lord Howe Island Marine Park (LHIMP) and Batemans Marine Park (BMP).
tures from this assumption for the sample sizes used in our study (Underwood 1997).

A 2-factor ANOVA was used to examine potential differences between years and sites within SIMP for any species determined by SIMPER analysis as being important contributors to differences (i.e. \( \%\delta_i > 3\% \) and \( \delta_i/SD(\delta_i) > 1 \)). Potential differences between years and sites in SIMP due to marine park zoning were also explored for *Pagrus auratus*, given the findings of other studies for this species (Willis et al. 2003).

**RESULTS**

Reef fish assemblage

A total of 101 species (44 families) were observed from SIMP (2006 data), PSGLMP and JBMP combined, representing 11 species (9 families) of Chondrichthyes and 90 species (35 families) of Osteichthyes, from various trophic groups including predators, herbivores and planktivores (Appendix 1). The fish family that was most speciose in our samples was Labridae (19 species). The Chondrichthyes sampled included 8 species of sharks and 3 species of rays. Species were accumulated at a similar rate, with increasing replication in each park, although accumulation curves did not reach an asymptote for any park (Fig. 2).

A total of 5874 individual fish was observed by combining MaxN data from all sets. The most abundant species were the schooling planktivores *Atypichthys strigatus* (Scorpididae, 1280 ind.), *Scorpis lineolata* (Scorpididae, 1137 ind.), *Trachurus novaezelandiae* (Carangidae, 971 ind.) and the predator *Ophthalmolepis lineolatus* (Labridae, 323 ind.). Twenty-seven species were observed only as single ind. (SIMP 9 species, PSGLMP 8 species, JBMP 10 species).

Spatial variation in assemblages between and within parks

Separation of parks on the nMDS ordination was consistent with their latitudinal distribution (Fig. 3). The fish assemblages of each park were significantly different (Table 1). The greatest dissimilarity in assemblage structure occurred between the most northern (SIMP) and southern (JBMP) parks. PSGLMP, located approximately midway between SIMP and JBMP, was equally dissimilar to both (Table 1). Fish assemblages also differed significantly between most sites within each park (Fig. 3, Table 1).

<table>
<thead>
<tr>
<th>PERMANOVA results parks</th>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
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<td>1121.23</td>
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</tbody>
</table>

<table>
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<tr>
<th>Average dissimilarity within/between parks</th>
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<th>SIMP</th>
<th>PSGLMP</th>
<th>JBMP</th>
</tr>
</thead>
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<td></td>
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<td>PSGLMP</td>
<td>43.16</td>
<td>24.20</td>
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</tr>
<tr>
<td>JBMP</td>
<td>51.41</td>
<td>40.04</td>
<td>33.51</td>
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Post hoc comparison of parks

<table>
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<tr>
<th>Comparison</th>
<th>t</th>
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<tbody>
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<td>SIMP vs. PSGLMP</td>
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<td>0.03</td>
</tr>
<tr>
<td>SIMP vs. JBMP</td>
<td>2.72</td>
<td>0.03</td>
</tr>
<tr>
<td>PSGLMP vs. JBMP</td>
<td>2.06</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Stress: 0.12

Fig. 2. Mean species accumulation curves for each park based on 1000 random selections (without replacement) of replicate samples. Park abbreviations: see Fig. 1

Fig. 3. nMDS plot, based on centroids of 4 sites within each park (△: Solitary Islands Marine Park, 2006; ×: Port Stephens-Great Lakes Marine Park; ●: Jervis Bay Marine Park) and previous yearly data for SIMP (+: 2002; ×: 2003; ◆: 2004; Δ: 2005).
Similar numbers of total species were recorded in SIMP (56 species), PSGLMP (60 species) and JBMP (60 species). More sharks and rays were recorded in PSGLMP (10 species) than in either SIMP in 2006 (5 species) or JBMP (5 species), or even SIMP over 5 yr (9 species). More species of Labridae were recorded in SIMP (14 species) than JBMP (10 species) or PSGLMP (4 species). More species of Monacanthidae were recorded in PSGLMP (8 species) and JBMP (7 species) (4 species). More species of Labridae were recorded in JBMP (5 species) or PSGLMP (5 species), or even SIMP over 5 yr (60 species). More sharks and rays were recorded in SIMP (56 species), PSGLMP (60 species) and JBMP (56 species).

SIMPER identified 13 species as being influential in differentiating the fish assemblages of the 3 parks (Table 2). Variation in the abundance of the common schooling species *Atypichthys strigatus* and *Scorpa lineolata* meant that they were consistently influential. Another common schooling species, *Trachurus novaezelandiae*, was an important contributor to all pairwise differences in assemblage structure and occurred in greatest numbers in PSGLMP. The girdled parma *Parma unifasciata* (Pomacentridae) was abundant only in SIMP, whereas the Port Jackson shark *Heterodontus portusjacksoni* (Heterodontidae) was not recorded in SIMP and differed in abundance between PSGLMP (average MaxN = 1.28) and JBMP (0.72). The snapper *Pagrus auratus* (Sparidae) was present, but varied in abundance in all parks (SIMP mean MaxN = 1.53, PSGLMP = 2.19, JBMP = 0.41).

**Spatial variation in species between and within parks**

Seven of the 13 species identified as being influential in differentiating the assemblages, differed at the park level, but not the site level (Fig. 4, Table 3). The relative abundance (mean MaxN) of *Scorpaena cardinalis* (Scorpaenidae) and *Parma unifasciata* decreased strongly with increasing latitude, with the latter not recorded at JBMP. *Parma microlepis* was only recorded at the southern parks, and found at both of these in similar abundances. The average number of *Heterodontus portusjacksoni* (Heterodontidae), *Nemadactylus douglasii* (Cheilodactylidae) and *Meuschenia freycineti* (Monacanthidae) differed between all 3 parks; all were found in greatest numbers at PSGLMP, followed by JBMP, then SIMP.

**Table 2. Overall dissimilarity (δ) in fish assemblages between parks (SIMPER). Species regarded as being important contributors to the assemblage dissimilarity are shown in bold. Values shown for each park in the pairwise comparisons are the average MaxN for the species. Park abbreviations: see Fig. 1**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>SIMP vs. PSGLMP</th>
<th>SIMP vs. JBMP</th>
<th>PSGLMP vs. JBMP</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Atypichthys strigatus</em></td>
<td>3.30</td>
<td>4.04</td>
<td>3.28</td>
</tr>
<tr>
<td><em>Parma unifasciata</em></td>
<td>2.84</td>
<td>3.54</td>
<td>0.10</td>
</tr>
<tr>
<td><em>Trachurus novaezelandiae</em></td>
<td>2.79</td>
<td>3.37</td>
<td>3.50</td>
</tr>
<tr>
<td><em>Meuschenia freycineti</em></td>
<td>2.40</td>
<td>1.09</td>
<td>2.08</td>
</tr>
<tr>
<td><em>Scorpa lineolata</em></td>
<td>2.26</td>
<td>2.65</td>
<td>2.09</td>
</tr>
<tr>
<td><em>Nemadactylus douglasii</em></td>
<td>2.24</td>
<td>1.85</td>
<td>1.90</td>
</tr>
<tr>
<td><em>Heterodontus portusjacksoni</em></td>
<td>2.13</td>
<td>1.84</td>
<td>1.90</td>
</tr>
<tr>
<td><em>Parma microlepis</em></td>
<td>1.85</td>
<td>1.77</td>
<td>1.64</td>
</tr>
<tr>
<td><em>Aulopus purpurissatus</em></td>
<td>1.83</td>
<td>1.33</td>
<td>2.11</td>
</tr>
<tr>
<td><em>Pagrus auratus</em></td>
<td>1.82</td>
<td>2.42</td>
<td>2.66</td>
</tr>
<tr>
<td><em>Parupeneus spilurus</em></td>
<td>1.79</td>
<td>0.60</td>
<td>1.94</td>
</tr>
<tr>
<td><em>Scorpaena cardinalis</em></td>
<td>0.77</td>
<td>3.30</td>
<td>2.60</td>
</tr>
<tr>
<td><em>Notolabrus gymnogenis</em></td>
<td>0.52</td>
<td>2.83</td>
<td>2.52</td>
</tr>
</tbody>
</table>
The relative abundances of 4 species varied significantly among sites, but did not differ among parks (Fig. 5A to D, Table 3). These included the most-abundant species, *Trachurus novaezelandiae*, *Scorpius lineolata* and *Atypichthys strigatus*. These schooling planktivores, along with *Pagrus auratus*, showed strong site differences at all parks, the exception of *S. lineolata* at PSGLMP. Two species, *Notolabrus gymnogenis* (Labridae) and *Aulopus purpurissatus* (Aulopidae), differed at both the park and site levels (Fig. 5E,F, Table 3).

### Temporal stability of fish assemblages in SIMP

A total of 88 species were recorded from 180 replicates in the SIMP from 2002 to 2006 (n = 36 replicates yr⁻¹). The total number of species recorded in each year was similar, with the average number of species per site per year ranging from 30.7 (±2.1 SE) to 32.5 (±1.3 SE). Individually, sites were more variable through time, with 1 site having a range of 9 species over the course of the study (Site 3: 25 species in 2004, 34 in 2006). The overall range from all sites for all years was 25 to 37 species. The number of additional species recorded in each subsequent year decreased from 13 in 2003 to 6 in 2006. The most speciose family recorded was Labridae. The number of labrid species was similar in all years (13 or 14 species), except for 2005 (9 species).

Table 3. Summary of results of 2-factor ANOVA testing for differences in MaxN of 13 species between parks and between sites within parks. *Cochran’s test p > 0.05

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Meuschenia treycinetia</em></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>79.45</td>
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<td>0.41</td>
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<td></td>
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<tr>
<td><em>Parupeneus spilurus</em></td>
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</tr>
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<td>2</td>
<td>14.07</td>
<td>64.33</td>
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</tr>
<tr>
<td>Site (Park)</td>
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<td>0.20</td>
<td>0.99</td>
</tr>
<tr>
<td>Residual</td>
<td>84</td>
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<td></td>
<td></td>
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<td><em>Parma unifasciata</em></td>
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<td><em>Scorpaena cardinalis</em></td>
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<td>0.40</td>
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<td>84</td>
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<td><em>Nemadactylus douglasi</em></td>
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<td><em>Notolabrus gymnogenis</em></td>
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<td><em>Parma microlepis</em></td>
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<tr>
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<td>1.67</td>
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</tr>
</tbody>
</table>

*ln(x+1) transformed, variances homogeneous*

Untransformed, variances heterogeneous*

Untransformed, variances homogeneous*

Fig. 5. Mean MaxN (±SE) at each site for 6 species that differed significantly in abundance between sites within parks.
Eight species of Osteichthyes were recorded at all 4 sites in all 5 yr (Appendix 1). These included *Noto- labrus gymnogenis* and *Ophthalmolepis lineolatus* (Labridae), *Gymnothorax prasinus* (Muraenidae), *Parma unifasciata* (Pomacentridae), *Hypoplectrodes maccullochi* (Serranidae), *Scorpaena cardinalis* (Scorpaeidae) and *Pagrus auratus* (Sparidae). Three species, *O. lineolatus*, *N. gymnogenis* and *P. unifasciata*, were recorded in 90, 87 and 83% of replicate sets, respectively. A number of other species were present at most sites in most years, including 2 Chondrichthyans, the blind shark *Brachaelurus waddi* (Brachaeluridae) and the ornate wobbegong *Orectolobus ornatus* (Orectolobidae). The 2 species that were numerically dominant, *Scorpis lineolata* and *Atypichthys strigatus*, were recorded at most sites in each year, but were patchy in their abundance between replicate sets within a site. Overall, there was a relatively stable assemblage of about 30 species within the total of 88 species observed. The remaining species included 17 that were incidentally recorded once, and 7 only that were recorded twice.

There was temporal stability in assemblages at the broad geographic or latitudinal scale, as SIMP was separated from the other parks on the nMDS ordination over the 5 yr studied, including years when surveys were undertaken in the other parks (Fig. 3). There were changes over time at the within-park scale, and these were not consistent by site. The assemblage structure changed significantly between successive years at all sites except Site 4, as shown by the significant Year × Site interaction (Table 4). Assemblages at Sites 1 to 3 changed dramatically in 2005 compared with previous years and 2006, as shown by the displacement of sample points for these sites to the right of the ordination plot (Fig. 6).

The SIMPER analysis found that no individual species contributed >3% to the average dissimilarity of any pairwise comparisons between either years or sites. A combination of 3 to 5 species together contributed 3% average dissimilarity for both. In comparisons between years this group included the midwater schooling species, *Atypichthys strigatus*, *Trachurus novaezelandiae* and *Prionurus microlepidotus* (Acanthuridae) and *Pseudocaranx dentex* (Carangidae), and the small benthic schooling hulafish *Trachinops taeniatus* (Plesiopidae). In 7 out of 10 pairwise comparisons, *A. strigatus* contributed the highest percentage to this dissimilarity. However, overall >35 species contributed >1% dissimilarity for all yearly pairwise comparisons; therefore, univariate analyses were not conducted to examine individual dissimilarity contribution.

*Pagrus auratus* was examined individually to explore potential underlying reasons for the year by site interaction, as 2 of the sites where there was an obvious

---

**Table 4. Summary of results of permutational multivariate analysis of variance (PERMANOVA) comparing assemblages of fishes over 5 yr (2002 to 2006) at 4 sites in SIMP, and post hoc pairwise comparisons of years at each site. *p < 0.05, **p < 0.01, ***p < 0.001**

<table>
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<th>p</th>
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<td>Year</td>
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<td>0.0004</td>
</tr>
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<td>Site</td>
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<td>9478.69</td>
<td>7.72</td>
<td>0.0002</td>
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<tr>
<td>Year × Site</td>
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<td>1.57</td>
<td>0.0004</td>
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<tr>
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**Post hoc comparison of years and sites (t, p)**

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<td>1.50</td>
<td>1.09</td>
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</tr>
<tr>
<td>2002 vs. 2004</td>
<td>1.49</td>
<td>1.48</td>
<td>1.37</td>
<td>1.11</td>
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<tr>
<td>2002 vs. 2005</td>
<td>2.12**</td>
<td>1.73*</td>
<td>1.49</td>
<td>0.91</td>
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<tr>
<td>2002 vs. 2006</td>
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<td>1.42</td>
<td>1.10</td>
<td>1.00</td>
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<tr>
<td>2003 vs. 2004</td>
<td>1.64</td>
<td>1.18</td>
<td>1.11</td>
<td>0.61</td>
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<tr>
<td>2003 vs. 2005</td>
<td>1.92**</td>
<td>2.31**</td>
<td>1.97**</td>
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<tr>
<td>2003 vs. 2006</td>
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<td>1.74*</td>
<td>1.09</td>
<td>1.23</td>
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<tr>
<td>2004 vs. 2005</td>
<td>2.57**</td>
<td>2.49***</td>
<td>1.98**</td>
<td>1.08</td>
</tr>
<tr>
<td>2004 vs. 2006</td>
<td>1.59*</td>
<td>1.64*</td>
<td>1.21</td>
<td>1.05</td>
</tr>
<tr>
<td>2005 vs. 2006</td>
<td>1.65*</td>
<td>2.11**</td>
<td>2.07**</td>
<td>1.06</td>
</tr>
</tbody>
</table>

---

**Table 5. Two-factor ANOVA testing for differences in MaxN of *Pagrus auratus*, between years and sites in SIMP; ln(x + 1) transformed, variance homogeneous (Cochran’s test p > 0.05) following transformation**

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<thead>
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<th>p</th>
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<td>7.71</td>
<td>28.12</td>
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</tr>
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<td>0.000</td>
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<td>Residual</td>
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<td>0.27</td>
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</table>
change in assemblage in 2005 were in sanctuary zones (Sites 1 and 2). MaxN for *P. auratus* showed a slight increase at Sites 1 and 2 from 2002 to 2004, increased considerably at Sites 1 to 3 in 2005, and then declined in 2006, but remained higher at Sites 1 and 2 in comparison to at Sites 3 and 4. This reflects the overall pattern detected by PERMANOVA (Table 5, Fig. 7).

**DISCUSSION**

As we observed significantly different fish assemblages in all parks, all 3 marine parks are necessary to representatively reserve samples of the reef fish biodiversity in NSW. While the degree of difference in fish assemblages between parks was consistent with the latitudinal gradient, species richness for particular families did not follow any general latitudinal pattern. For instance, Labridae were more diverse in the north, but still diverse with different species in the south, while the Monacanthidae were more strongly represented in the 2 most southern parks. We also found strong temporal stability, over a 5 yr period at SIMP, in the assemblage of reef fish relative to our broader geographic observations.

**BRUVS as a technique for sampling reef fish assemblages**

BRUVS is a useful method for comparing and assessing reef fish assemblages on coastal rocky reefs (15 to 30 m depth) across a range of spatial and temporal scales. With our BRUVS we detected the expected bioregional differences in assemblage structure between 3 widely spaced marine parks, as well as variation at the scale of 2 to 20 km. These scales of spatial variation are similar to those detected by UVC techniques (Curley et al. 2002, Anderson & Millar 2004) on shallower rocky reef. The significance of spatial variation in the abundance of schooling planktivores for differentiating assemblages detected by our study has also been reported for assemblages of reef fishes described by UVC (Curley et al. 2002).

Although fish bait was used to attract predators and scavengers, a cross-section of the overall reef fish community was sampled, representing a range of trophic guilds including herbivores and planktivores (Appendix 1). This agrees with other BRUVS surveys, where fish attracted to bait or commotion, as well as those passing through or residing in the immediate vicinity, were observed (Cappo et al. 2004, Watson et al. 2005, Stobart et al. 2007). The taxonomic composition of the fish fauna was also similar to that reported from diver surveys from comparable locations in eastern Australia, with Labridae and Monacanthidae being the most speciose families (Parker 1999, Barrett et al. 2006, Gladstone 2007).

BRUVS is a powerful technique for detecting cryptic scavengers. For example, green moray eels *Gymnothorax prasinus* appear to be more widespread and abundant in the study area than UVC surveys have previously indicated (Curley et al. 2002, Barrett et al. 2006, Gladstone 2007). Although this may be due to UVC surveys being conducted in shallower depths, shallower BRUVS surveys in JBMP suggest this is not the case (J. Wraith unpubl. data). Differences in methods may be more pronounced for cryptic scavengers/predators that generally reside within the reef matrix, and are unavailable for counting by divers, than for those that rely on camouflage. In SIMP, for example, the cryptic *G. prasinus* and blindshark *Brachaelurus waddi* were not recorded from UVC in 10 to 15 m depth, whereas the well-camouflaged wobbegong shark *Orectolobus ornatus* was recorded from 14% of transects (H. Malcolm unpubl. data). By comparison, the same species were recorded in 61, 26 and 33%, respectively, of BRUVS replicates, although in slightly deeper water. Benthic sharks and rays are generally poorly sampled by UVC techniques. Our study recorded 12 species (9 families) of Chondrichthyans. In contrast, an intensive UVC survey of a section of the NSW coast near PSGLMP recorded only 3 species of Chondrichthyans (Gladstone 2007). Trophic transfer through these scavengers/predators on reefs in NSW is poorly understood, but they are likely to be highly important given their abundance and the even distribution revealed in our surveys.

There are a variety of potential issues with the use of BRUVS to describe fish assemblages, which include the sampling requirements to reach species accumulation asymptotes and the influence of factors that vary on a small time scale. Based on our species accumulation curves not reaching asymptote, and from additional species being recorded each year in SIMP, further sampling will detect more species. Fourteen
Significant spatial variation and latitudinal influences

Significant variation in assemblages at a range of spatial scales is typical of reef fishes (Curley et al. 2002, Anderson & Millar 2004, Garcia-Charton et al. 2004, Gladstone 2007). Spatial variation in assemblage structure at large spatial scales may reflect various influences, including biogeography (Edgar et al. 2004), latitude (Bouchon-Navaro et al. 2005), geology (Guidetti et al. 2004), depth, temperature and productivity (Leathwick et al. 2006). At the scale of our NSW marine parks study, the greatest dissimilarity in assemblage structure occurred between the most northern (SIMP) and southern (JBMP) parks, which were separated by 603 km. The middle park, PSGLMP, located halfway between the others, was equally dissimilar to both.

A change in species composition and number was also expected along this latitudinal gradient (Gray 2000); however, similar numbers of total species were recorded in each park (56 to 60 species). There were also differences in higher taxon composition between the parks that did not relate to a latitudinal gradient. For example, twice as many shark and ray species were recorded in PSGLMP than in either SIMP or JBMP, and more species of Monacanthidae were recorded at JBMP and PSGLMP than at SIMP. The species richness of Labridae was bimodal, with peaks at the most northern and southern parks. Combinations of biogeographic, oceanographic and environmental factors are probably responsible for these patterns. For example, the restricted biogeographic distributions for some of the Chondrichthyes endemic to eastern Australia (Last & Stevens 1994) have influenced the greater species richness observed for this fauna at PSGLMP, by overlapping of subtropical and temperate endemic species (Appendix 1). This overlap may also be reflected in observed family richness, which was greatest in PSGLMP (36) versus SIMP and JBMP (30 and 32, respectively). Australia has more species of Monacanthidae than any other region of the world, with many confined to temperate waters (Randall et al. 1997), and again this biogeographic pattern was reflected in this study. Fish species with a tropical/sub-tropical distribution recorded in SIMP were important in terms of increasing species richness in particular families, and for individual species representation. However, they were less influential than was expected (Meekan & Choat 1997) in distinguishing the SIMP assemblage from the other parks using this method. Given that the species most important in differentiating between these parks are abundant, and have a distribution that includes all parks (Kuiter 2000), it is possible that assemblage differences could be attributable to large-scale environmental differences that affect populations of many species (Williams 1991).

Significant spatial variation in fish assemblages occurred between sites inside each marine park, i.e. at the scale of kilometres. Spatial variation in assemblage structure of fishes at relatively small spatial scales (100s to 1000s of metres) may relate to combinations of variation in habitat structure (Connell & Jones 1991, Willis & Anderson 2003), recruitment (Connell & Jones 1991, Lincoln Smith et al. 1991), local hydrodynamics (Warner et al. 2000), or other influences. Although variation at these scales was less than at the between-park scale, it indicated some sites (within a park) were more similar than others, and these similarities/differences appeared to be independent of the distance between them, as has been found in other studies (Gladstone 2007).

Temporal variation and stability in patterns

From the 5 yr of data from SIMP, we consistently sampled a relatively stable fish assemblage of about 30 species with many of the other 58 species rarely
recorded. This is consistent with the findings of other studies where a large number of the species constitute a small percentage of the number of individuals sampled, and most species are relatively rare (Jones et al. 2002).

The fish assemblage over time was less stable at the site scale, and there was a consistent shift at most of the sites in 2005. Differences between years and sites within SIMP were, like most of our park-wide variation, driven by schooling planktivores, especially *Atypichthys strigatus*. The difference in 2005 could be due to a range of factors, including environmental conditions, influencing that particular year, or causing short-term variability at a temporal scale not examined, such as weeks. For instance, there was a heavy swell in the weeks preceding sampling in 2005 that may have influenced the assemblage at each site. However, the sampling at Site 1 was repeated 3 wk later with similar results (H. Malcolm unpubl. data). Sea temperature logger records (Malcolm 2007) did not indicate any major differences that would separate 2005 from other years in SIMP, but, given the greatest dissimilarity was due to schooling mid-water planktivores, changes in plankton associated with food resources could have had an influence. If so, this may have been due to localised influences rather than wider processes associated with the El Niño weather pattern. The Southern Oscillation Index (SOI) was close to zero at the time of sampling in 2005, and had generally been in a weak El Niño pattern since mid-2004 (NOAA 2007).

There was a distinct increase in abundance of *Pagrus auratus* at 3 sites in 2005, with changes in other years that closely reflected the overall PERMANOVA pattern. Therefore, the processes that underpinned this increase in *P. auratus* may have also influenced other species. This could have included good recruitment in previous years, as strong inter-annual pulses in *P. auratus* may have been demonstrated (Fowler & Jennings 2003, Hamer & Jenkins 2004). Marine Park zoning may have also influenced these results as both MaxN and the proportion of sets containing *P. auratus* remained higher at 2 sites in 2006, where fishing has been prohibited since 2002. Again, this is not unexpected as strong benefits of sanctuary zones to snapper populations have been previously demonstrated (Willis et al. 2003, Denny & Babcock 2004). However, variation in abundance of species such as *P. auratus* can occur within and between years (Willis et al. 2003), and caution is needed in attributing the extent that marine park management has influenced these results. To adequately answer the question of sanctuary zone effectiveness, which was not an aim of the present study, further sampling over a longer time frame is required.

**CONCLUSIONS**

Overall, the information provided by BRUVS indicates that the 3 marine parks include different assemblages of fishes on rocky reef at 15 to 30 m depth. Incorporating natural patterns of variability in assemblages of reef fishes should be a goal of a representative network of marine parks (Lubchenco et al. 2003, Gladstone 2007), and these 3 marine parks contribute towards that goal. Our results also support the existence of bioregions for the fish fauna of shallow coastal reefs in NSW and their use as a basis for MPA planning. However, rocky reef extends down to at least 120 m depth in NSW, and the spatial patterns of reef fish assemblages below 30 m are unknown. This study therefore encourages the further application of BRUVS as a technique to investigate the assemblages of fishes in deeper coastal reefs, both inside and outside of marine parks to further examine representation.

BRUVS is also useful for indicating which marine parks are important for representing particular families when used in combination with other methods. As an example of higher taxon representation in marine parks, SIMP may be particularly valuable to conservation of the diversity of Labridae and the southern parks of JBMP and PSGLMP may be important for conservation of the diversity of Monacanthidae. The PSGLMP may also be of importance for conserving the diversity of Chondrichthyes, as this particular rich and abundant chondrichthyan fauna, with a high level of endemism, is unique to rocky reefs in south-eastern Australia (Last & Stevens 1994).

The present study has demonstrated that BRUVS is a repeatable method that can be used to detect patterns over time at both assemblage and species levels. It, therefore, has application as a monitoring tool, providing sampling is undertaken at suitable multiple temporal and spatial scales that will enable environmental and management influences to be partitioned.

**Acknowledgements.** Our research was sponsored by the NSW Marine Parks Authority. We thank B. Vercoe, R. Thorman, T. Waters, N. Johnstone, V. Mansbridge, A. Jordan, N. Brown, I. Osterloh and M. Fackerell for assistance in the field. Thanks also to M. Cappo for technical advice, and V. Mansbridge for GIS support. Thanks to A. Jordan, B. Creese and the anonymous reviewers for very helpful comments on an earlier version of this manuscript.

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Last PR, Stevens JD (1994) Sharks and rays of Australia. CSIRO, Melbourne


### Appendix I. Species recorded by BRUVS at the Solitary Islands Marine Park in 2006 (SIMP–06), Port Stephens–Great Lakes Marine Park in 2006 (PSCMP), and Jervis Bay Marine Park (JMP, 2005). A species recorded by Year and by Site within SIMP. Numeric values are mean MaxN for each marine park if not recorded. Distribution—E: endemic; R: regional; C: cosmopolitan; Cir: circumglobal; with (description) indicating area. Trophic grouping—H: herbivore; Pl: planktivore; Ben: predator non-mobile invertebrates & infauna; Pred: predator of mobile invertebrates/fishes; Pis: dedicated piscivore; Om: omnivore (Ben/Pred/H); Scav: dedicated scavenger (versus opportunistic); Zoo: zooplankton; ?: assumed, but not positive. Distributions and trophic groupings taken from taxonomic references (Last & Stevens 1994, Randall et al. 1997, Kuiter 2000).

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<table>
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<td>Pl (Zoo)</td>
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<td>Scorpaena</td>
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ABSTRACT: The relatively unobtrusive deep-sea camera system Eye-in-the-Sea (EITS) was deployed in Monterey Bay Canyon, California, USA, to assess the relative photosensitivity of 2 deep-sea fishes, Coryphaenoides acrolepis and Anoplopoma fimbria. Previous studies addressing the in situ response of deep-sea fishes to red and white light were done in the presence of ROV-induced stimuli. Here, we report on the behavioral response of C. acrolepis and A. fimbria in a vehicle-free environment when subjected to white (full visible spectrum), red (685 nm), and far-red (695 nm) illumination in situ. Under far-red light conditions, A. fimbria spent significantly more time in the field-of-view and demonstrated an increase in entrances/exits when compared to the situation under red-light and white-light conditions. No significant difference in the average time C. acrolepis spent in the field-of-view was found between any of the test wavelengths; however, the entrances-to-exits ratio for C. acrolepis decreased during white-light conditions. While A. fimbria often displayed a flight response at the onset of white and sometimes red (685 nm) illumination, C. acrolepis did not demonstrate a similar behavioral response when exposed to light within its range of visual sensitivity. A. fimbria undergo a dramatic ontogenic shift in depth, inhabiting well-lit, near-shore waters as juveniles and moving into deeper waters as adults. It is thought that C. acrolepis spend part of their early life history in the light-limited mesopelagic, below the permanent thermocline, and move into deeper waters as they mature. Based on the results of the present study, we hypothesize that systematic differences in the phototactic responses of deep-sea fishes are a function of life history as well as spectral sensitivity.

KEY WORDS: Deep sea · Red light · Fish behavior

INTRODUCTION

High pressure, lack of light, and limited access to deep collection sites all present serious challenges to the sampling and/or observation of deep-sea fishes (Smith & Baldwin 1997). Difficulty in net-sampling deep-sea fishes without significant modification or damage to their physiology has generally precluded laboratory-based behavioral studies. In situ collection methods (e.g. submersibles, remotely operated vehicles [ROVs]), on the other hand, rely on bright white (full visible spectrum) lights, which may cause irreversible retinal damage to the animal of interest (Douglas et al. 1995, Herring et al. 1999). Sampling devices such as traps, which block out light while maintaining constant pressure and temperature, have proven valuable (Childress et al. 1978, Phleger et al. 1979, Wilson & Smith 1985), but typically involve small sample sizes and small specimens/species. As a result, arguments have been made for the value of in situ video and still imagery capture via vehicle-free or ‘lander’ systems (Phleger & Soutar 1971, Priede & Merrett 1996, Priede et al. 1998). Baited cameras are highly effective at attracting scavengers and subsequent predators, which may be drawn in by the resulting chemosensory and perhaps mechanosensory stimuli (Wilson & Smith 1984, Smith 1985, Priede & Smith 1986, Henriques et al. 2002). Many of the vehicle-free camera systems

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used to obtain images of the deep are also equipped with bright white illuminators; however, these illuminators are typically used as intermittent strobes and likely result in only a periodic effect (Wilson & Smith 1984, Priede et al. 1998). Red light as a form of unobtrusive illumination has been employed in multiple shallow-water studies (Jury et al. 2002, Mills et al. 2005) and a few deep-sea studies (e.g. Widder et al. 2005).

In the present study a relatively unobtrusive video observation system, the Eye-in-the-Sea (EITS) (Widder et al. 2005) was used to record the response of deep-sea animals to different wavelengths of light in situ. The vast majority of deep-sea fishes possess a single visual pigment, with maximal sensitivity in the blue-green region of the visible spectrum (Douglas et al. 1995), which coincides with the available wavelengths of light from attenuated surface radiance and bioluminescence (Denton 1990). Electrophysiological, morphological, and some behavioral studies have indicated that most deep-sea fishes have limited sensitivity to longer wavelengths (Partridge et al. 1988, Douglas & Partridge 1997, Widder et al. 2005). However, a few genera (Pachystomias, Aristostomias, and Malacosteus) in 1 family of meso-/bathypelagic fishes, are known to produce far-red bioluminescence and to have long-wave visual sensitivity (O’Day & Fernandez 1974, Widder et al. 1984, Bowmaker et al. 1988, Partridge et al. 1989, Partridge & Douglas 1995), and the possibility cannot be discounted for some others (Douglas et al. 2002).

Widder et al. (2005) demonstrated that the deep-sea fish Anoplopoma fimbria (sablefish, Anoplopomatidae) responded to red light in situ even though this species has a maximum visual sensitivity at 491 nm (Ali & Wagner 1975). From these results it appeared that sablefish were able to detect long-wave (680 nm) light; although, how far into the far-red spectrum that sensitivity extended was not clear. Widder et al. (2005) carried out observations with a single illuminator, making it impossible to test the response of deep-sea fishes to >1 wavelength of illumination during a given deployment. In order to overcome this limitation, we added an additional illuminator to the EITS system for the purposes of comparing effects of different wavelengths of illumination.

Here, we describe the behavioral response of 2 deep-water species, the Pacific grenadier Coryphaenoides acrolepis (Macrouridae) and the previously mentioned sablefish Anoplopoma fimbria to white, red, and far-red illumination. Both species were frequently recorded at our study sites in Monterey Bay, California, USA. C. acrolepis is a common benthopelagic, mid-slope species (Cohen et al. 1990) thought to spawn at depth (Phleger 1971, Stein & Pearcy 1982). Buoyant eggs float up to depths below 200 m and develop in the midwater until settling in the benthopelagic as juveniles. Studies suggest that, compared to the well-developed olfactory system, vision may play a minor role in the feeding strategies of certain adult macrourid species, such as C. armatus (Wagner 2002, 2003). One proposed explanation for the large eyes of adult macrourids is to locate the perianal light organ of potential mates (Okamura 1970). A. fimbria, also benthopelagic, is found in surface and near-shore waters during early life-history stages and migrates to deeper waters as adults (Armstrong 1996).

In order to assess the relative photosensitivity of these species, we recorded their behavior when subjected to white, red (λmax = 685 nm), and far-red (λmax = 695 nm) illumination in situ.

**MATERIALS AND METHODS**

**Equipment.** EITS, Ver. 2.0, was used to record deep-sea video during this study. EITS is an autonomous deep-sea viewing platform designed for deployment down to 1000 m from a ROV or submersible (Fig. 1). The basic EITS system consisted of red-light illumination in conjunction with an intensified camera, photomultiplier tube (PMT) trigger, an onboard computer, data storage, and custom-programmable software. In order to compensate for the low-light conditions due

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**Fig. 1.** *In situ* image of Eye-in-the-Sea (EITS) deployed in Monterey Bay, California. Bait was attached to the framework of the cannibalized ladder alignment mechanism (CLAM) and inserted into the bait box. Image provided by MBARI/ROV ‘Ventana’. Viewing platform length: 2.5 m, height: 2.2 m
to red-light attenuation, an intensified CCD camera (ITT 880, ITT Industries Corporation) with extended sensitivity in the blue range was used. The camera was fitted with a 2.54 cm f/0.95 lens, with a fixed focal length of 25 mm.

Ancillary devices on the EITS included an electronic jellyfish (E-jelly) capable of imitating 5 different luminescent displays, and a hydrophone. While on deck, the EITS’s data storage and software program were accessible through an Ethernet communication port. All parameters (illuminators, E-jelly, recording period and frequency, time and trigger mode) were fully programmable by the user. Video from the CCD camera was streamed to an onboard PC-104 capture card and stored directly on an 80 GB hard drive using a MPEG 4 compression format. The system was mounted on an aluminum tripod frame and powered by a 24 V rechargeable, lead acid Seabattery (DeepSea Power & Light) (Fig. 1). A bait box was fastened to a foldable bait alignment frame, the cannibalized ladder alignment mechanism (CLAM), 2 m away from the camera (Fig. 1). During the present study, 2 independently operated LED illuminators were used. Illuminators were fitted with red LEDs (685 nm), red LEDs with a high-pass filter (695 nm), or white LEDs.

Spectral measurements. The spectral irradiances of the EITS’s red illuminators were measured in air with a spectroradiometer (OL 754 UV-Vis, Optronic Laboratories). Each red illuminator package comprised of 40 red (685 nm) LEDs and an optional filter slot. A long wave pass filter glass substitute (Corion), with a peak transmission at 711 nm, was used to reduce short-wavelength emissions. White illuminators consisted of 35 white LEDs. Illuminators were aligned on an optics bench 2 m away from the spectroradiometer and powered by a 12 V DC/1 amp bench-top power supply. Spectral irradiance of the white, red, and far-red illuminators were recorded (400 to 750 nm) at 5 nm intervals.

Using Smith & Baker’s (1981) diffuse attenuation coefficients, $K$, for irradiance in the clearest ocean waters, irradiance at 2 m from the illuminators in water, $E_{\text{a}}(\lambda)$, was calculated as:

$$E_{\text{a}}(\lambda) = E(\lambda) e^{-Kz}$$

where $z$ is the distance from the illuminator and $E(\lambda)_a$ is the in-air irradiance, from 400 to 750 nm at a distance of 2 m.

In water the red illuminator had a peak irradiance of $2.47 \times 10^{-7}$ W cm$^{-2}$ nm$^{-1}$ at 685 nm, and the far-red illuminator had a peak irradiance of $1.64 \times 10^{-8}$ W cm$^{-2}$ nm$^{-1}$ at 695 nm, whereas the white illuminator had a broad spectral distribution with a peak irradiance of $9.03 \times 10^{-9}$ W cm$^{-2}$ in the blue region (465 nm) (Fig. 2). Total irradiance values for white, red, and far-red illuminators were $1.4 \times 10^{-7}$, $1.35 \times 10^{-6}$, and $7.51 \times 10^{-8}$ W cm$^{-2}$, respectively.

**Study sites and experimental conditions.** During fall 2005, spring 2006, and fall 2006, the EITS was deployed at 3 sites in Monterey Bay for a total of 6 dives (Table 1). All deployments were done with Monterey Bay Aquarium Research Institute’s (MBARI) hydraulically powered ROV ‘Ventana’, deployable to depths of 2300 m. The ROV’s swing arm stabs (suspension arms) held the camera in position during the deployment and recovery dives. Deployments were made using baited traps and the E-jelly optical lure. Carcasses from local fish species
were used as bait. Fish heads and backbones were strapped to the CLAM's black aluminum frame. Larger chunks of fish flesh were placed in a flow-through black plastic bait box, which had 6.0 mm wide slits along the sides and top. When possible, the system was aligned so that direction of Camera view was across-current at the time of deployment. The system was programmed to run in both timed and timed/triggered mode. Upon recovery, all video clips were downloaded from the EITS to a topside laptop computer and stored for later analyses. The EITS was programmed to record for 1 min at 5 min intervals, starting during the ROV deployment period. The program ran until the EITS was recovered or the system’s battery life was exceeded, typically 30 to 36 h after deployment on the seabed. Illuminators were programmed to turn on at the start of the 1 min recording period and turn off at the end of the 1 min recording period. Red-light experiments consisted of 1 min of red illumination every 5 min over a 30 min interval, followed by 1 min of far-red illumination for the same recording interval. This program (red, dark, red, red followed by far-red, dark, far-red, dark) was repeated multiple times throughout each mission. A white- versus red-light experiment was conducted in the same manner, but using far-red and white illumination. Although the E-jelly ran during portions of Dives 4 and 5, it was programmed to remain off during the red-light experimental period.

**Video analysis.** Only video clips from the timed mode and in the absence of the ROV were used in these analyses. A total of 1150 MPEG 4 video clips of 1 min each were analyzed. Type and number of deep-sea species were recorded. When Coryphaenoides acrolepis or Anoplopoma fimbria were present (Fig. 3), 3 activities were noted in each 1 min block for both species: (1) time spent in the field-of-view, (2) the number individuals entering the field-of-view, and (3) the number of individuals exiting the field-of-view. Due to differences in depth-of-field between the white, red, and far-red illuminators, only fish swimming between the camera and the bait container at the end of the CLAM were used in the final analyses, in order to standardize the volume viewed between the 2 different viewing regimes. The field-of-view in this study was defined as 2 m deep by 0.84 m wide. Data from closely spaced deployments in time at the same study site were pooled for analysis. Statistical analysis was performed applying WinStat® statistical software for Excel. The Kruskal-Wallis test was used to test for a normal distribution. Data were not normally distributed, and differences in time spent in the field-of-view during periods of unfiltered (685 nm) and filtered (695 nm) illumination were analyzed for significance using the Mann-Whitney U-test. Values were considered significant at p < 0.05.

**RESULTS**

**Species present at study sites.** With the exception of Eptatretus deani (black hagfish), Anoplopoma fimbria was the most common fish species present on Dives 1, 2, 3, and 5, whereas the most abundant megafauna during Dives 4 and 6 was Coryphaenoides acrolepis. During each study period, the number of individuals for all species present fluctuated over time. *A. fimbria* were frequently present early in the deployment period, but tended to drop off in numbers over time. Often they would reappear in pulses later in the deployment period. A similar pattern was detected in *C. acrolepis*. In addition to *C. acrolepis, A. fimbria,* and *E. deani,* other fish species seen around the study site included Somniosus pacificus (Pacific sleeper shark), Antimora microlepis (finescale mora), and Apristurus sp. (cat shark). Since these species were observed infrequently, they were not included in the quantitative behavioral analysis.

**Coryphaenoides acrolepis activity in red light.** A Mann-Whitney U-test on the average amount of time *C. acrolepis* spent on camera in the presence of red versus far-red illumination indicated there was no sig-
significant difference (Fig. 4a). Moreover, there was no prominent difference in the ratio of C. acrolepis entrances to exits between illumination conditions (Fig. 4b). Under both illumination conditions, C. acrolepis appeared undisturbed and, unless bumped by another individual, rarely displayed startled behavior.

Since a current meter was unavailable during this study, drift direction of marine snow and loose pieces of bait were used as an indicator of current direction. It was observed that most of the macourids aligned themselves with the current and approached the bait from the down-current direction. Once Coryphaenoides acrolepis approached the CLAM, they would frequently maintain a position downstream of the bait container, with their heads pointing upstream.

**Anoplopoma fimbria activity in red light.** Data from Dives 2 and 3 revealed a significant difference in the average time A. fimbria spent in the field-of-view under the 2 illumination conditions (Fig. 4c). Although there was no statistical difference (p = 0.28) in average time on camera during Dives 4 and 5, there was a considerable difference in entrances to exits, indicating a tendency for A. fimbria to avoid the study site under red illumination. Throughout Dive 4, A. fimbria were not present in the field-of-view during periods of red illumination. A. fimbria data had a consistent pattern of smaller ratios of entrances to exits during periods of red illumination (Fig. 4d). To test the effect of changes in illumination intensity at the same wavelength on fish behavior, we fitted both illuminators with the 711 nm filter and used them simultaneously during the 1 min recording periods on Dive 1. During this experiment, the average amount of time individual A. fimbria were detected in the field-of-view, 16.7 s, was comparable to the single illuminator at 695 nm average, 17.4 s, on Dive 2, but lower than the average of Dive 3, 23.7 s.

Four primary behavioral patterns were observed for Anoplopoma fimbria: (1) rapidly swimming through the field-of-view, which was commonly seen during the initial deployment period; (2) active and aggressive feeding on the bait; (3) a rapid turn in swimming direction or abrupt cessation of feeding within the first 1 or 2 s of red illumination; and (4) a slow meandering around the periphery of the circle of illumination when the red illuminator was on. Aggressive feeding behavior was most prevalent during, but not limited to, periods of far-red illumination.

**White-versus red-light experiments.** Both Coryphaenoides acrolepis and Anoplopoma fimbria were observed at the study site during Dive 6. The swimming pattern of A. fimbria was noticeably different during periods of white illumination. A. fimbria were frequently observed darting outside the field-of-view at the onset of the white illumination period. For A. fimbria there was a significant decrease in average time spent on camera during white-light exposure; however, in the C. acrolepis assemblage there was no significant difference in the average time spent in the field-of-view between light treatments (Fig. 5a). A decrease in the entrances-to-exits ratio during periods of white light was observed in both species (Fig. 5b), indicating an avoidance of the study site under white-light illumination.

**DISCUSSION**

Analysis of Anoplopoma fimbria and Coryphaenoides acrolepis swimming behavior during periods of white, red (685 nm), and far-red (695 nm) illumination indicated that both species respond minimally to longer wavelengths of red light; however, responses to these wavelengths of light were species specific.
**Anoplopoma fimbria** often spent significantly more time in the field-of-view during periods of far-red illumination, whereas *C. acrolepis* behavior was not statistically different when exposed to shorter and longer wavelengths of red light. The decrease in *A. fimbria* time on camera during red- and white-light conditions is consistent with their known range of visual sensitivity in situ (Widder et al. 2005).

Results from the present study show that deep-sea fishes tend to avoid regions of illumination within their range of detection. The entrances-to-exits ratio was used as a species-specific proxy for the degree of response to illumination wavelength. A ratio well below 1 indicated aversion to each wavelength, whereas a high ratio (>1) indicated attraction to specific wavelengths. *Anoplopoma fimbria* assemblages consistently had lower entrances-to-exits ratios during periods of red- or white-light illumination, while ratio values close to 1 during exposure to far-red light indicate minimal disturbance or detection at that wavelength of illumination. *A. fimbria* were frequently observed skirting the field-of-illumination’s periphery under white and red conditions, but we did not note the same type of avoidance behavior from individual *Coryphaenoides acrolepis* during any illumination condition. Although entrances-to-exits ratios for *C. acrolepis* did not indicate a strong behavioral response to the red wavelengths used in this study, there was a slight decrease in the ratio values when white light was present.

The visual systems of *Anoplopoma fimbria* and *Coryphaenoides acrolepis* have adapted to the spectral quality of the depths they inhabit. The intensity and spectral quality of light changes with depth, and, in optically clear waters, blue light travels the furthest (Jerlov 1976). Since deeper waters are devoid of red light, with the exception of biologically produced red light, which is made available by a very limited number of fish species (Widder et al. 1984), visual pigments of deep-sea fishes have a wide absorption spectrum and, as a result, capture light from a broad emission range (Bowmaker et al. 1994). Below depths where sunlight can penetrate, bioluminescence is the only source of illumination. Montgomery & Pankhurst (1997) make the argument that the type of visual sensitivity required for surface light detection in the mesopelagic zone is also well adapted for detection of bioluminescence in the aphotic zone. *A. fimbria* undergo a dramatic ontogenic shift in depth. As juveniles, *A. fimbria* live in well-lit, near-shore surface waters and move off shore and into the light-limited environment of the deep sea as adults (Armstrong 1996). Life in such a dynamic depth range and light regime (Armstrong 1996) requires a broad sensitivity spectrum. Conversely, *C. acrolepis* primarily inhabit depths devoid or nearly devoid of sunlight. The flight reaction we observed in *A. fimbria* during periods with shorter wavelengths of light could potentially be a hardwired response as a method of predator avoidance in the well-lit surface waters during early development. This could also explain why we do not seem to see the same type of response from a deep-dwelling species like *C. acrolepis*.

*Anoplopoma fimbria* actively avoid white illumination compared to red illumination. This study confirms findings by Widder et al. (2005) that *A. fimbria* respond adversely to periods of white illumination as indicated by a decrease in the average time on camera and a lower ratio of entrances to exits. In a study by Wilson & Smith (1984), *Coryphaenoides* spp. behavior appeared unaltered by the presence of white illumination, as it was shown not to act as an attractant in the absence of bait nor did it deter fish from the viewing area during baited studies. The *C. acrolepis* present in this study were not attracted to the field-of-view during white-light conditions, and the decreased ratio in entrances to exits demonstrated avoidance during this time. Presented with white illumination clearly within their range of detection, *C. acrolepis* do not appear to respond to the same degree as *A. fimbria*. In the adult stages of life, certain macrourid species likely rely on olfaction and mechanoreception to find food sources and possibly use vision to find mates or, to a lesser extent, food (Wagner 2002, 2003). Bailey et al. (2007) suggested that grenadiers use olfaction to locate food sources from a distance, but rely on gustation and mechanoreception at close ranges to the source. It is possible that vision plays a minor role in the feeding ecology of adult *C. acrolepis*.

*Coryphaenoides acrolepis* and *Anoplopoma fimbria* are frequently observed around artificial food falls (Isaacs & Schwartzlose 1975, Smith 1985). Drazen et al. (2001) suggested that scavenged material may be an important component in the diet of adult *C. acrolepis* and could account for up to 20% of their total food consumption. Laboratory experiments conducted by Smith (1978) using hyperbaric chambers have revealed low metabolic rates in macrourids. Limited food availability in deep-sea benthic zones and predator avoidance are competing factors in metabolic requirements. *A. fimbria* are capable of sustaining long periods of food deprivation (Sullivan & Smith 1982), likely an adaptation to the periodic nature of food availability in the deep sea. Lokkeborg et al. (1995) demonstrated that response to a low-concentration odor plume was higher in food-deprived *A. fimbria*, whereas satiated individuals spent the majority of their time resting on the bottom, away from the light during periods of exposure to odor plumes. We propose that the observed *A. fimbria* behavior around our baited camera was the result of competing sensory inputs. During
periods of white and red illumination, vision outweighed olfactory cues; however, at wavelengths near the upper limit of their sensitivity range, A. fimbria were influenced primarily by olfaction and their level of starvation.

One of the limitations of red-light illumination in the ocean is the decreased range compared to white-light systems. We worked around this shortcoming by using an intensified camera. This solution had the added benefit of enabling us to record in situ naturally bioluminescent events. Bioluminescent events were rarely detected during timed recording periods and were normally the result of mechanical disturbances during feeding events. Sea whips Halipetris californica and sea pens Umbellula sp. were likely the main sources of observed bioluminescence.

Intensity of the red-illumination source dropped by more than an order of magnitude with the addition of the 711 nm high-pass filter. Although we limited analyzed observations to a distance of 2 m from the camera, fauna were often detected at greater distances from the system. In previous deployments, in which both illuminators were fitted with high-pass filters and operated in unison, a greater field-of-view of up to 4 m from the camera was possible, and there was no discernable difference between the average amount of time Anoplopoma fimbria spent in the field of view under different levels of intensity at the same wavelength (695 nm). Future deployments will involve the use of both illuminators fitted with high-pass filters given that 2 far-red illuminators provide sufficient lighting and species observed to date appear minimally affected by this illumination.

Based on the results of the present study, the benefits of the EITS 2.0 system for deep-ocean behavioral experiments are: (1) it is a relatively unobtrusive viewing platform, free from ship noise and white light; (2) it can be positioned to view specific areas of interest, including fragile habitats such as thickets of deep coral; (3) it can be equipped with up to 3 light sources of different wavelengths and programmed to come on in different combinations; and (4) it can be deployed for multiple days at a time. There are tradeoffs between attenuation of light in water, camera sensitivity, and animal sensitivity when conducting unobtrusive observations in the deep sea. Data presented here and in Widder et al. (2005) suggest that, although lower wavelengths of red light are detectable by some deep-sea species, far-red light (695 nm) is sufficiently unobtrusive for most deep-sea applications.

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