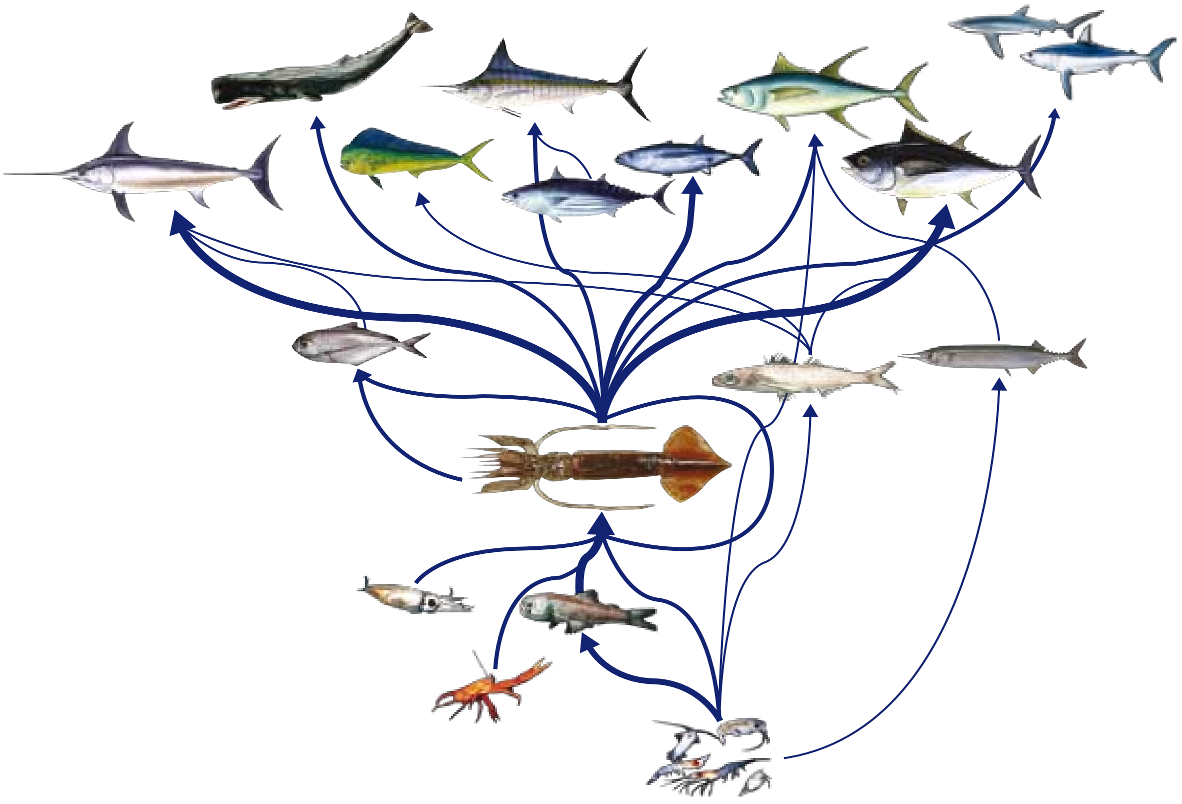
GLOBAL OCEAN ECOSYSTEM DYNAMICS

GLOBEC Report No.24

THE ROLE OF SQUID IN OPEN OCEAN ECOSYSTEMS

Report of a GLOBEC-CLIOTOP/PFRP workshop,
16-17 November 2006, Honolulu, Hawaii, USA

Robert J. Olson and Jock W. Young (Eds.)



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PREFACE

This report documents a workshop that was held under the auspices of CLIOTOP Working Group 3: Trophic Pathways in Open Ocean Ecosystems. The workshop was co-sponsored by GLOBEC, the Pelagic Fisheries Research Program (PFRP) of the University of Hawaii, USA; the Inter-American Tropical Tuna Commission (IATTC), California, USA; and the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Tasmania, Australia, and hosted by the PFRP. The workshop was held on 16-17 November 2006. It aimed to summarise relevant information on pelagic squid, and address how changing oceanographic conditions may affect squid's central role as prey and predator in open-ocean ecosystems.

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Robert J. Olson and Jock W. Young (Eds.). 2007. The role of squid in open ocean ecosystems. Report of a GLOBEC-CLIOTOP/PFRP workshop, 16-17 November 2006, Honolulu, Hawaii, USA. GLOBEC Report 24: vi, 94pp.

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LIST OF ABBREVIATIONS AND ACRONYMS

ARIMA	Autoregressive Integrated Moving Average Models
ARMA	Autoregressive-Moving Average
AVHRR	Advanced Very High Resolution Radiometer
BSR	Body Size Relationship
CalCOFI	California Cooperative Oceanic Fisheries Investigations
CLIOTOP	CLimate Impacts on Oceanic TOp Predators
DFA	Dynamic Factor Analysis
DHA	Docosahexaenoic Acid
ENFA	Ecological Niche Factor Analysis
ENSO	*El Niño* Southern Oscillation
EPA	Eicosapentaenoic Acid
FMSY	Fishing Mortality at MSY
GAM	Generalised Additive Model
GAMM	Generalised Additive Mixed Modelling
GIS	Geographic Information System
GLM	Generalised Linear Model
GLOBEC	Global Ocean Ecosystem Dynamics
IATTC	Inter-American Tropical Tuna Commission
ICPMS	Inductively Coupled Plasma Mass Spectrometry
IPO	International Project Office
IRI	Index of Relative Importance
LME	Large Marine Ecosystem
LRL	Lower Rostral Lengths
MDS	Multi-Dimensional Scaling
ML	Mantle Length
MSY	Maximum Sustainable Yield
NAO	North Atlantic Oscillation
OML	Oxygen Minimum Layer
OTN	Ocean Tracking Network
PFRP	Pelagic Fisheries Research Program
POST	Pacific Ocean Shelf Tracking
PSAT	Pop-up Satellite Archival Tags
PUFA	Polyunsaturated Fatty Acid
RAPD	Random Amplification of Polymorphic DNA
SST	Sea Surface Temperature
STFZ	Sub-tropical Frontal Zone
STL	Seasonal and Trend decomposition using Loess
TZCF	Transition Zone Chlorophyll Front

ABSTRACT

This report summarises, via a series of extended abstracts, a workshop to examine current research on the ecological role of squid in ocean ecosystems worldwide. The workshop was held at the University of Hawaii, Honolulu, 16-17 November 2006. The workshop was sponsored by GLOBEC/CLIOTOP and the Pelagic Fisheries Research Program (PFRP), University of Hawaii, and was organised as a contribution from CLIOTOP Working Group 3 (Trophic Pathways in Open Ocean Ecosystems). The workshop was attended by 37 participants from 9 countries. Twenty one talks and five posters were presented.

Four themes, biology and ecology, climate impacts, trophic links, and modelling, were addressed in a series of presentations followed by theme discussions moderated by a nominated specialist in that theme. The workshop concluded with a combined session which attempted to identify the major outcomes, challenges, and areas for future research, particularly in relation to climate change.

Because of the dramatic rise in the biomass of the jumbo squid, *Dosidicus gigas*, since 2000, there was a significant focus on this species during the workshop, particularly on its role as an indicator species in relation to potential scenarios of ocean warming. Research on other species, particularly from the families Ommastrephidae and Loliginidae, was also presented. Topics included distribution and abundance, fisheries, trophic relationships, laboratory studies, and modelling.

The workshop identified a number of research gaps, particularly the lack of long term data sets, and the paucity of research in the Indian and Atlantic Oceans. One of the central points to emerge was that the difficulty of capturing squid generally was a major impediment to understanding their role and importance in ocean ecosystems. As such, new methodologies are needed to develop a better understanding of this fauna. To this end, a number of new methodologies were detailed. In particular, research showing the value of satellite and archival tagging in understanding the movement and behaviour of these animals was presented. A variety of biochemical techniques, including fatty acid and stable isotope analysis showed promise in identifying the ecological role of squid in a broader spatial and temporal context.

The workshop ended with a number of recommendations for future research, which are summarised at the end of the report.

ACKNOWLEDGEMENTS

The convenors and editors thank Dr Manuel Barange (GLOBEC IPO) and Dr John Sibert (PFRP, University of Hawaii) for their encouragement and sponsorship of this workshop. We also thank Ms Dodie Lau and Mr Johnoel Ancheta (PFRP), for their assistance in organising and running the workshop; Mrs Lotty Dunbar (GLOBEC IPO) for organising travel for participants, and Miss Dawn Ashby (GLOBEC IPO) for her assistance in publishing this report. Funding from GLOBEC and PFRP and support from IATTC and CSIRO are gratefully acknowledged.

Finally, we are grateful to the enthusiasm of the attendees and their willingness to provide the very informative extended abstracts of which this report is comprised.

INTRODUCTION

The GLOBEC regional programme CLIOTOP (Climate Impacts on Oceanic Top Predators) has the central aim to identify, characterise, and model the key processes governing the dynamics of oceanic pelagic ecosystems leading to "top" predators, such as tunas, billfishes, mammals, and seabirds. The goal is to develop an improved understanding of the impact of climate variability and fishing on the upper trophic levels, and a reliable predictive capability for single species and ecosystem dynamics at short-, medium-, and long-term scales (Maury and Lehodey, 2005). Prerequisite for this goal is an understanding of the components and structure of pelagic ecosystems, and an appreciation of how changes in the pelagic environment will affect what we consider to be the status quo. CLIOTOP Working Group 3 (Trophic Pathways in Open Ocean Ecosystems) developed a number of objectives to understand the trophic pathways that underlie the production of tunas and other oceanic predators, including 1) the characterisation of the main trophic pathways of oceanic top predators and how they differ among and within oceans, and 2) identifying evidence for changes in trophic pathways over time and space, while considering seasonal and spatial variability.

The traditional pelagic food web model on which much of our understanding of ecosystem interactions is based is a conceptual pyramid, with large pelagic fishes at the top and preying on increasingly complex groups of organisms at lower trophic levels, and supported by primary production at the base. Cephalopods play a central role in many, if not most, marine pelagic food webs by linking the massive biomass of micronekton, particularly myctophid fishes, to many oceanic predators. Given the high trophic flux passing through the squid community, a concerted research effort on squid is critical to advancing our understanding of their role as key prey and predators.

Renewed interest in squid-ecosystem dynamics is motivated by recent remarkable range expansions of Humboldt or jumbo squid (*Dosidicus gigas*) in the eastern Pacific Ocean (e.g. Field and Baltz, p.55 this volume; Arancibia and Neira, p.68 this volume; Zeidberg and Robison, 2007), and speculation whether climate variability and/or fishing on squid predators could have promoted the increase. Characterised by short life spans and fast growth rates, squid may respond more readily to changes in the environment and in the trophic structure than perhaps any other mid-trophic-level organism in the open ocean.

In spite of their importance in pelagic ecosystems, squid are not well understood. In part, this is because of their ability to largely avoid capture by conventional marine sampling techniques. Other factors, such as their complex taxonomy compounded by their relatively fast digestion in predator stomachs, have meant that detailed information on their role in many ocean ecosystems is lacking. New technologies, including those able to track squid movements (e.g. archival and satellite tags) and new biochemical techniques capable of identifying squid presence in the tissues of their predators (e.g. stable isotope and fatty acid analysis), are helping to resolve some of the questions surrounding squid.

With encouragement and sponsorship from GLOBEC-CLIOTOP and the Pelagic Fisheries Research Program (PFRP)[1] of the University of Hawaii, a workshop was held on 16-17 November 2006 at the Hawaii Imin International Conference Center at the University of Hawaii immediately following the PFRP Principal Investigators Meeting. This workshop brought together squid ecologists working in diverse ecosystems and oceanographic regions from the Pacific, Atlantic, and Indian Oceans. It

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[1] The Pelagic Fisheries Research Program (PFRP) was established in 1992 after the Magnuson Fishery Conservation and Management Act (1976) was amended to include "highly migratory fish." This amendment greatly increased the responsibilities of the Western Pacific Regional Fishery Management Council, which is mandated to manage fisheries in the Western Pacific region. The PFRP was created to provide scientific information on pelagic fisheries to the Council for use in development of fisheries management policies. For further information on PFRP visit http://www.soest.hawaii.edu/PFRP/pfrp1.html.

aimed to summarise relevant information on pelagic squid - addressing how changing oceanographic conditions may affect squid's role as prey and predator.

Workshop topics included:

- consideration of the role of squid in pelagic ecosystems supporting tunas and other upper-level predators;
- consideration of how climate change might impact squid populations and the ecosystem;
- consideration of the recent range expansions of *D. gigas* in the eastern Pacific Ocean, especially in terms of the effects of such expansions on the various ecosystems;
- identification of the research needs addressing pelagic squid required to meet the goals of GLOBEC-CLIOTOP, and the identification of potential research proposals.

The workshop was attended by 37 participants from 9 countries. Twenty-one oral and five poster presentations were made by researchers from numerous countries, including: Australia, Canada, Chile, France, Great Britain (including the Falkland Islands), Japan, Mexico, Portugal and the USA (both east and west coasts). The workshop featured four main themes: biology and ecology, climate impacts, trophic links, and modelling. A final session, led by the moderators from each theme, reviewed the outcomes from each theme and highlighted potential future research.

This report provides extended abstracts from most of the presentations and contains summaries of the discussions and conclusions at the workshop.

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BIOLOGY AND ECOLOGY

Horizontal and vertical migrations of *Dosidicus gigas* in the Gulf of California revealed by electronic tagging

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Squid of the family Ommastrephidae, migratory predators of the open seas, are ecologically and economically important on a global scale. *Dosidicus gigas* (jumbo or Humboldt squid), the largest ommastrephid (up to 50 kg mass and mantle length of 1.2 m), is endemic to the productive waters of the eastern Pacific, particularly those of the California Current, Peru Current and Costa Rica Dome (Nigmatullin *et al*., 2001; Waluda and Rodhouse, 2006). This species is the target of the world's largest cephalopod fishery, with landings of 800,000 tonnes in 2004 (ftp://ftp.fao.org/fi/stat/summary/a1e.pdf).

Despite the commercial importance of *D. gigas*, relatively little is known of its natural behaviour. This squid grows extremely rapidly, increasing from 1 mm mantle length at birth to 1 m in a life-span of only 1-2 years (Nigmatullin *et al*., 2001; Markaida *et al*., 2004). Such a high growth rate requires a correspondingly large dietary intake, and the squid standing stock in the Guaymas Basin in the Gulf of California (Fig. 1), probably consumes ~107 kg (104 tons) per day (Gilly *et al*., 2006a). In this region, prey consists of mostly small mesopelagic fishes, crustaceans and other squid (Markaida and Sosa-Nishizaki, 2003).

Dosidicus gigas is also a vital prey species. As juveniles, these squid are preyed on by numerous pelagic fishes (particularly tunas) and birds throughout the eastern Pacific, as described by several papers in this volume. In the Gulf of California, adult *D. gigas* serves as prey for both very large fishes (Klimley *et al*., 1993; Abitia-Cardenas *et al*., 2002; Rosas-Aloya *et al*., 2002) and marine mammals, particularly pilot and sperm whales (Ruiz-Cooley *et al*., 2004; 2006). Thus, jumbo squid provide an important trophic link between small mesopelagic organisms and vertebrate apex predators.

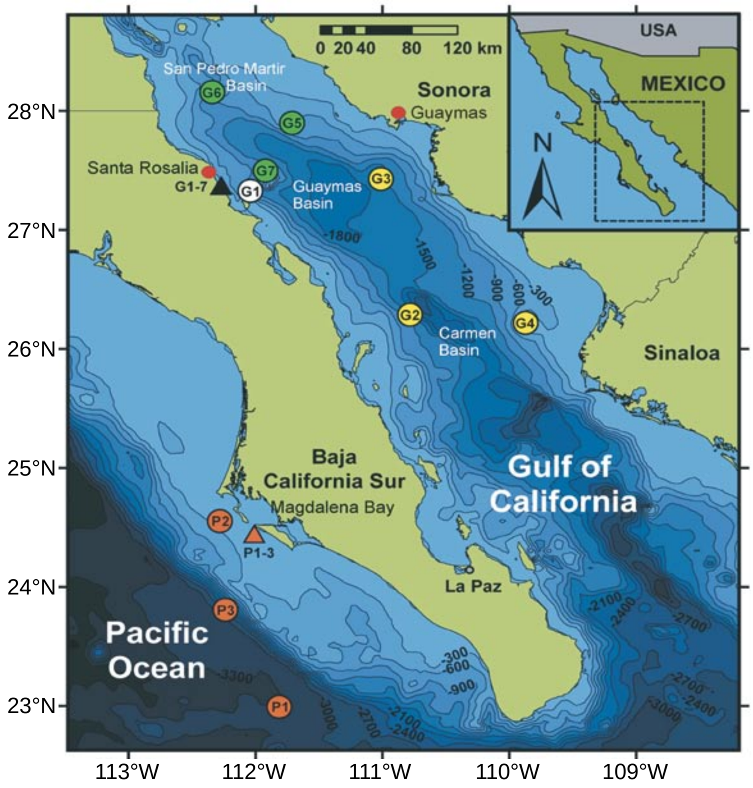

Figure 1. Tagging locations of *Dosidicus gigas*. Black triangle off Santa Rosalia marks deployment site for PSAT's G1-G7 (Wildlife Computer PSAT 3.0); pop-up locations are shown in yellow (October 2004) and green (November 2005) circles. Other tags deployed off Magdalena Bay in June 2005 (P1-P3) are denoted by red triangle and individual red circles. Data from these tags are not discussed in this report.

Commercial fishing operations for *D. gigas* began in the late 1970s and have since increased dramatically in both the northern and southern hemispheres. The bulk of the Mexican fishery (~100,000 tonnes or 20% of the world total) is located in the Guaymas Basin of the Gulf of California (Fig. 1), a relatively small area where commercial fishing is centred around the ports of Santa Rosalia (June-November), and Guaymas (Markaida and Sosa-Nishizaki, 2001). Conventional tag-and-recapture studies (Markaida *et al*., 2005) demonstrated a seasonal migration from Santa Rosalia to Guaymas in November, and a reciprocal migration in May, but routes and rates of migration remain poorly understood.

As a way of addressing migratory behaviour of *D. gigas* in the Guaymas Basin, we have utilised electronic archiving tagging methods, primarily pop-up satellite archival tags (PSAT). In September 2001, we deployed the first PSAT off Santa Rosalia (G1, Fig. 1), and 3 additional tags were deployed in October 2004 (G2-G4). Pop-up positions of the 2004 tags revealed that squid could migrate at least 200 km in one week, 3-4 times faster than the speed previously estimated (Markaida *et al*., 2005). Secondly, the direction of migration was to the southeast (G2, G4) or east (G3). Although the direction of squid G3 seems appropriate for a migration to the Guaymas fishing grounds, the direction taken by G2 and G4 does not. This south-westward movement may represent a migration out of the Gulf and into the Pacific, or to regions of the Gulf that are presently not subject to commercial fishing. Squid G1, tagged earlier in the autumn, remained in the vicinity of Santa Rosalia.

Three squid tagged in 2005 migrated to the north (G6) or northeast (G5), covering distances of ~100 km in 3 days. The end-point of squid G7 was ambiguous. Migration speeds were thus comparable to those observed in 2004, but the direction was essentially opposite to that seen previously. If squid G5-G7 were making a Santa Rosalia to Guaymas migration, it would appear that the route passes through the San Pedro Martir Basin and then turns south. A seasonal current in this part of the Gulf shows similar directionality and timing (Alvarez-Borrego, 2002), and the current switches back to a counter clockwise circulation in late spring, roughly in phase with the May migration from Guaymas to Santa Rosalia. This current could thus serve to both guide and ease migrations. Alternatively, some squid may migrate from Santa Rosalia in November to the San Pedro Martir Basin and remain there (Gilly *et al*., 2006b).

Time-at-depth data from the PSATs consistently showed that *D. gigas* spent daytime hours at depths of ~300 m, whereas night-time hours tended to be spent at much shallower depths (<150 m) (Fig. 2). A night-time component was also evident at typical daytime depths. One month of time-series data from an archival tag deployed in September 2004 directly revealed frequent rapid excursions between the shallow night time zone and deep daytime zone (Fig. 3). In addition, rhythmic episodes of diving activity were prominent during both day and night at both deep and shallow depths. We believe that these excursions are related to foraging activity in at least two ways. Firstly, squid appear to forage (i.e. rhythmic diving) at night both in the shallow zone and at depth (as well as in the daytime). Secondly, they may also make deep night-time dives to recover from thermal stress encountered while foraging in warm surface waters. These ideas are discussed elsewhere in greater detail (Gilly *et al*., 2006a; Davis *et al*., 2007).

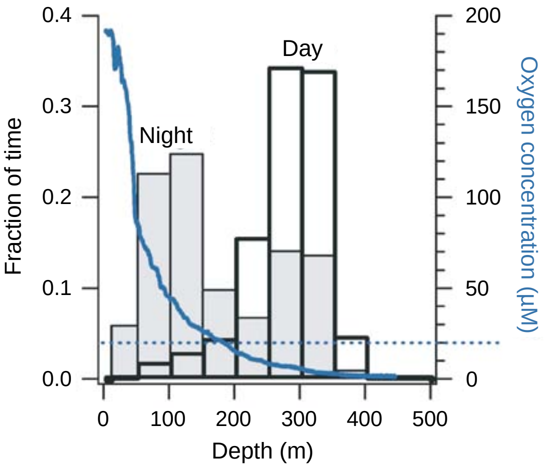

Figure 2. Diel change in vertical distribution of *D. gigas* as revealed by PSAT tags. Time-at-depth histograms are illustrated for mean data from tags G5-G7 (November 2005). Open bars are daytime hours (local sunrise to sunset); grey bars are night-time hours. Fraction of time was computed separately for day and night. Data were collected in 1 hour bins. The blue curve represents the dissolved oxygen profile recorded at the site of tag deployment one day later. Dotted blue line represents upper boundary of the OML (~20 µM concentration).

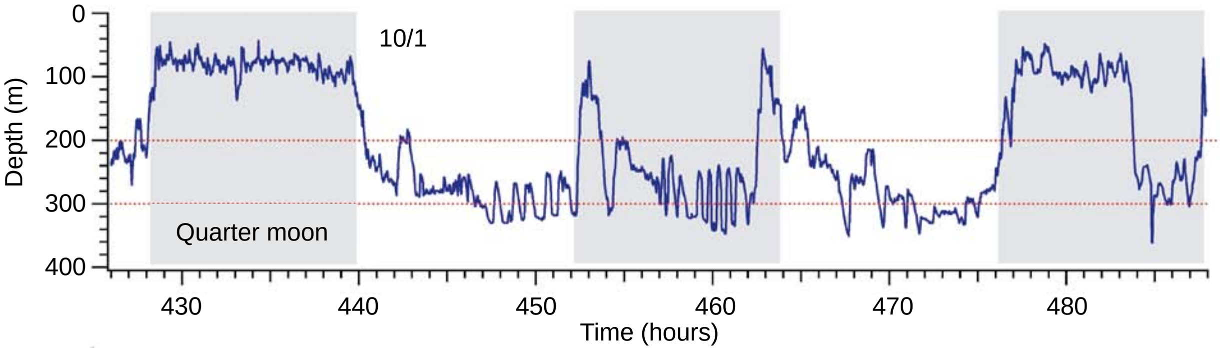

Figure 3. Complex diving behaviours from a squid carrying an archival tag (Lotek 1100) deployed at the same site as that for PSAT's (September - October 2004, sampling time was 2-4 min). The plotted hour refers to cumulative time after release. Night-time hours are indicated by shaded areas; lunar phase is indicated. The 200-300 m zone bounded by dotted lines represents the upper boundary of the OML. Much high-frequency diving occurs in this hypoxic zone both day and night.

Daytime depths revealed by tagging in the Santa Rosalia area are associated with a midwater hypoxic environment, the oxygen minimum layer (OML). Mean vertical distributions (day and night) computed for Tags G5-G7 are compared in Figure 2 with an oxygen profile taken 1-2 days later in the same area after deploying the tags. The dotted blue line indicates an oxygen concentration of 20 µM, our operational definition of the upper boundary of the OML. These squid regularly inhabited depths with a lower oxygen content, i.e. deeper than ~175 m.

These initial tagging experiments have increased our understanding of fundamental aspects of the biology of *D. gigas* concerning both horizontal migrations and daily vertical movements into the hypoxic environment of the OML. The apparent ability of this squid to maintain high levels of muscular activity at hypoxic depths while foraging and/or migrating is remarkable and is difficult to reconcile with what is known about the respiratory physiology of other active squid, including ommastrephids (Pörtner, 2002). Efforts are now underway to investigate this phenomenon in more detail, including relevant physiological and biochemical mechanisms.

Tagging has also yielded insights into horizontal migrations. The finding that the November migration (Tags G5-G7) from Santa Rosalia to Guaymas may involve passage through the San Pedro Martir Basin, or perhaps to this spot as a terminal destination, is particularly interesting. This area is essentially unexplored with regard to squid and is not commercially fished (Gilly *et al.*, 2006b). Although many questions about long-distance migrations remain unanswered, the application of PSAT methods is clearly feasible and should be more extensively applied, both in the Gulf of California and in the Pacific Ocean. Choice of times and places for tagging will be important.

Our results show that *D. gigas* utilises the hypoxic OML to an unexpected extent. Foraging probably occurs day and night, shallow and deep. Vertical migrations are likely to represent essentially continuous searching for patches of abundant prey, with rhythmic bouts of diving activity reflecting active foraging on myctophids and other members of the mesopelagic community associated with the deep acoustic scattering layer and the OML. Although the mechanisms underlying the ability to withstand hypoxic stress remain to be elucidated, the fact remains that this squid spends much time in an environment that is hostile to predatory pelagic fishes. Inhabiting the OML may protect juvenile or smaller *D. gigas* from predation by these fishes, but penetration of this habitat by the largest adults is likely to be the portal to foraging grounds from which pelagic predators like tunas are essentially excluded.

Physiological adaptations and flexible behaviour of *D. gigas* must also underlie its apparent ability to rapidly exploit environmental perturbations resulting from ENSO events and other thermal anomalies, as well as hypoxia anomalies (Grantham *et al.*, 2004). Such events alter productivity and may create transient windows of opportunity for *D. gigas* to expand its range (Bakun and Broad, 2003). If an area into which expansion occurs remains highly productive, the squid are likely to remain there and eventually make another excursion from the new starting point. If the area is not productive enough to support *D. gigas*, the squid will retract or find another ephemeral hot spot. Because of its extremely fast growth and migratory nature, *D. gigas* provides an extremely rapid indicator of environmental changes.

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Distribution of *Dosidicus gigas* paralarvae off the west coast of the Baja California peninsula, Mexico

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Squid from the Ommastrephidae family represent an important component in marine ecosystems, and are targeted by commercial fisheries in many coastal and pelagic waters of the world (Yatsu, 2000). This family also contributes substantially as a food item in the diet of predators, such as procellariiform seabirds, tunas, sharks, and over 80% of the odontocete species (Weimerskirch, 1995; Clarke, 1996). In Mexico, a single species of this family, the jumbo flying squid *Dosidicus gigas*, is the main component of the commercial squid catches. In spite of the social and economic value of this resource in our country, the identification of the early life stages of these squid still represents an acute problem. One of the objectives of our study was to identify the paralarvae of this species, and their distribution and abundance off the west coast of the Baja California Peninsula.

All cephalopod paralarvae were sorted from zooplankton samples collected with standard Bongo net tows in September 1997 (9709) and January, July and October 1998 (9801, 9807, and 9809, respectively) as part of the IMECOCAL programme, which covered the area from Ensenada, BC to Punta Abreojos BCS, Mexico (Fig. 1). The ommastrephid paralarvae (Pl) were sorted from the samples and identified based on the characteristic proboscis of the family. Ommastrephid Pl constituted about 1.3% in September 1997 to 82.5% in July 1998 of the total abundance of cephalopods in the study area (Fig. 2a), and were represented by four species identified for the first time along the west coast of Baja California, Mexico: *Dosidicus gigas*, *Sthenoteuthis oualaniensis*, *Eucleoteuthis luminosa*, *Hyaloteuthis pelagica*, two morphotypes (A and B), and a group of very small (<3 mm mantle length) Pl of *D. gigas* and/or *S. oualaniensis* from a recent spawning event ("S-D group"). Among these ommastrephids, *D. gigas* dominated in abundance by far during the study period (756 Pl/1000 m^3). The highest abundance of this species was found during July 1998, with

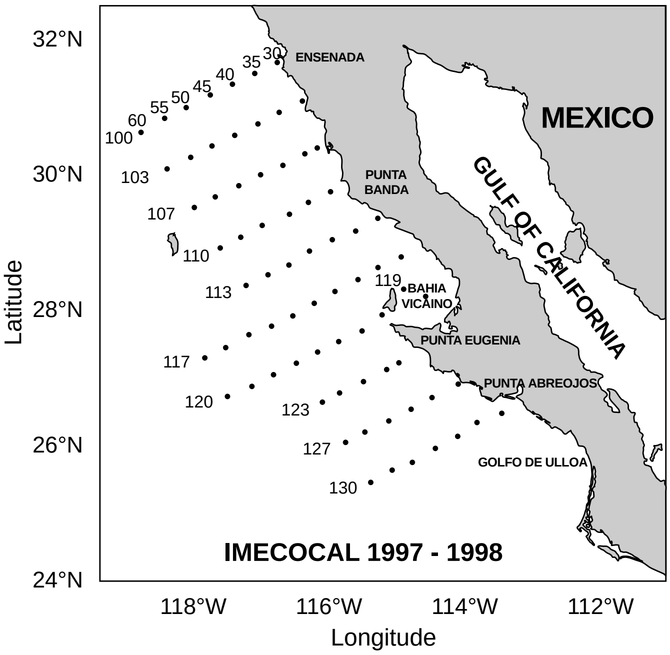

Figure 1. Study area and location of sampling stations.

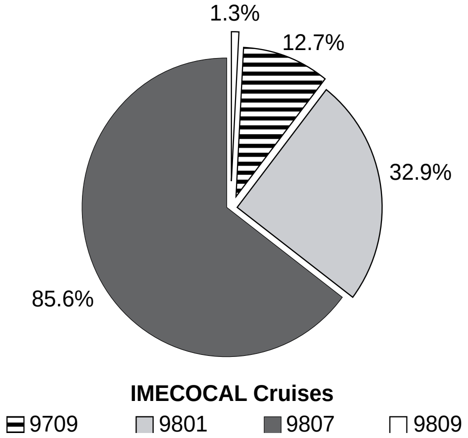

Figure 2a. Relative abundance of the Ommastrephidae paralarvae collected during the study period (cruise 9709 was in September 1997 and cruises 9801, 9807 and 9809 were in January, July and September 1998).

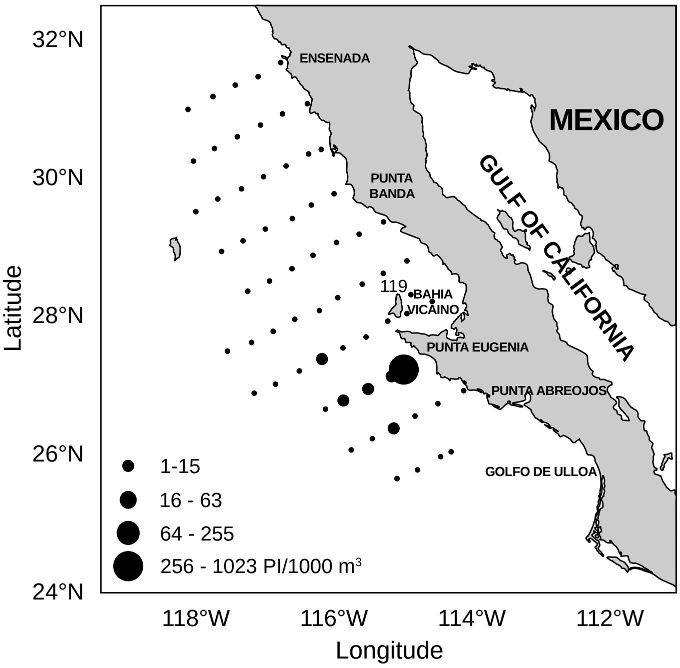

Figure 2b. Distribution and abundance of *Dosidicus gigas* paralavae during July 1998 (cruise 9807), along the west coast of the Baja California peninsula, Mexico.

more than 90% of the paralarvae distributed within 50 km of the coast off Punta Eugenia (Fig. 2b). Paralarvae of *D. gigas*, as well as those of the S-D group, consistently were present in the south region of the study area and were collected at stations sampled at sunrise (0600 h). *Dosidicus gigas* paralarvae were captured at stations where the temperature at 10 m depth ranged between 19.5° and 22°C, with a peak at 20.5°C, while the S-D group was captured at temperatures ranging from 18.5° to 22.5°C, with a peak also at 20.5°C. During the study period, the 1997-1998 El Niño event, the most intense in history, was recorded in Mexican waters (Durazo and Baumgartner, 2002). Two different water masses were recognised by these authors according to their spiciness (π) values: Subarctic Water mass (SAW) ($\pi<0.6$), and Transitional-Subtropical Surface Water mass (TrStSW) ($\pi>1.5$). The paralarvae of the *D. gigas* and S-D group were associated with the TrStSW, and with the boundary between both water masses ($\pi=1$).

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Cephalopod metabolism as a function of body size

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The inverse relationship between mass-specific metabolic rates and body mass, most famously illustrated by the ‘mouse to elephant curve’ for mammals, covering six orders of magnitude size range, is among the most established in all of biology (Schmidt-Nielsen, 1984; Calder, 1984). Metabolic rate (B) typically decreases with increasing mass (M) according to:

$$B = b_0 M^b$$

where b_0 is a normalisation constant independent of mass and the exponent, b, is a scaling coefficient. Both b_0 and b are reportedly highly conserved, such that metabolic rates can be modelled from only mass and temperature. However, here we show wide variation in both parameters within the class Cephalopoda related to geometrical and ecological attributes of individual species (Table 1; Fig. 1).

Ommastrephid and loliginid squid (Fig. 1), including the jumbo squid, *Dosidicus gigas*, are highly active species with metabolic rates that fall closely along a single scaling curve. The rates of larger squid are unmatched by any organisms of similar size. Metabolic rates decline with depth in pelagic cephalopods such that deep-sea species (e.g. *Vampyroteuthis infernalis*) have rates similar to gelatinous zooplankton (Seibel *et al*., 1997; Seibel, 2007). Deep-sea hypometabolism can be explained, not by constraints associated with a seemingly inhospitable environment (hypoxia, low temperature, high pressure or food limitation), but rather by strong selection for locomotory capacity in well-lit surface waters and a relaxation of such selection in the light-limited deep-sea (Seibel *et al*., 1997; Seibel, 2007).

The variation in scaling coefficients (b) may arise from the unique geometric allometry in tube-shaped oceanic squid. Mantle diameter increases faster than thickness with consequent growth in surface area with size (O’Dor and Hoar, 2001). Increasing surface area supports extensive cutaneous oxygen uptake, as is required to meet even resting oxygen demand (~60%; Pörtner, 2002). Also of importance, cost of transport for jet-propelled squid may not decrease as fast as that for other forms of locomotion (e.g. fin swimming fishes, O’Dor and Webber, 1986). High sustained energetic requirements (to grow and reproduce) during all stages of the squid’s short life cycle is another trait unique to squid that increases relative cost at large sizes (for more discussion see Glazier, 2006; Seibel, 2007). These three factors all reduce the potential energy savings associated with large size that we believe results in the commonly reported negative allometry of mass-specific metabolism in animals.

Table 1. Oxygen consumption rates (B; µmoles O_2 g^{-1} h^{-1}, 5°C) in cephalopods as a function of body mass (M) ($B = b_0 M^b$)

Family	b (SE)	b_0	r^2	n
Loliginidae	-0.084 (0.010)	8.20	0.56	51
Ommastrephidae	-0.077 (0.015)	7.60	0.60	20
Gonatidae	-0.02 (n.s.)	4.57	n.s.	24
Octopodidae	-0.27 (0.054)	3.35	0.90	15
Histioteuthidae	-0.24 (0.083)	1.36	0.58	26
Cranchidae	-0.19 (0.089)	0.53	0.31	33
Bolitaenidae	-0.25 (0.072)	0.27	0.66	32
Vampyroteuthidae	-0.23 (0.115)	0.14	0.56	17

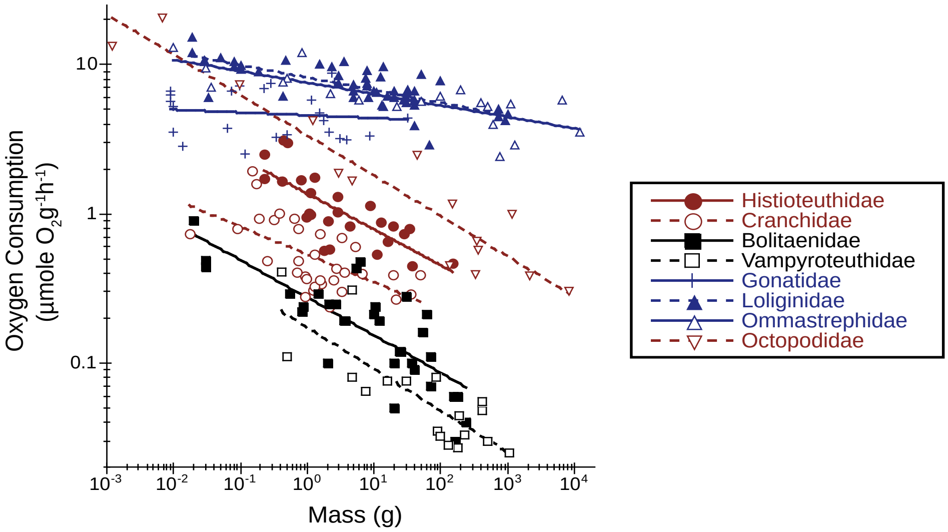

Figure 1. Oxygen consumption rates of cephalopod families as a function of body mass.

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Metabolism of jumbo squid *Dosidicus gigas* as a function of CO_2 concentrations

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The absorption of atmospheric carbon dioxide (CO_2) causes ocean acidification, i.e. decreasing pH. Business as usual emission scenarios are expected to cause a reduction in global ocean pH by more than 0.3 units by the year 2100. This constitutes a doubling of the hydrogen ion concentration (Caldeira and Wickett, 2003) and is expected to have severe consequences for calcifying organisms, among others. Squid are hypothesized to be sensitive to elevated CO_2, as their respiratory protein is often characterised by a pronounced Bohr coefficient (Pörtner, 2002). That is, a small decrease in pH will impair oxygen transport. However, the effects of environmentally-relevant pH reduction on the marine biota are still poorly understood (Seibel and Fabry, 2003). We investigated the impact of short-term hypercapnia (0.1% CO_2, up to 24 hours), equivalent to a tripling of pre-industrial levels, on the oxygen consumption rates of juvenile squid, *Dosidicus gigas*. We also measured mass-specific rates of oxygen consumption under normoxic and normocapnic conditions (MO_2; µmoles O_2 $g^{-1}h^{-1}$) in *D. gigas*.

The rates we measured were similar to rates reported for other ommastrephids and to the coastal loliginids (Seibel, 2007). However, they were higher than those of fishes and even mammals (at comparable size and temperature), a fact that reflects the low efficiency of jet propulsion relative to other forms of locomotion (Webber and O'Dor, 1986). After acidifying seawater by bubbling an air mix with 0.1% CO_2 (the concentration expected to be attained in the oceans in 100 years), the standard (SMR; between 4 and 21 µmol h^{-1} g^{-1}), routine (RMR, between 5 and 26 µmol h^{-1} g^{-1}) and active (AMR; between 7 and 38 µmol h^{-1} g^{-1}) metabolic rates (Fig. 1) showed a steady decrease of approximately 10-25% with high CO_2 levels. However, these effects were not significant (ANCOVA, $P > 0.05$).

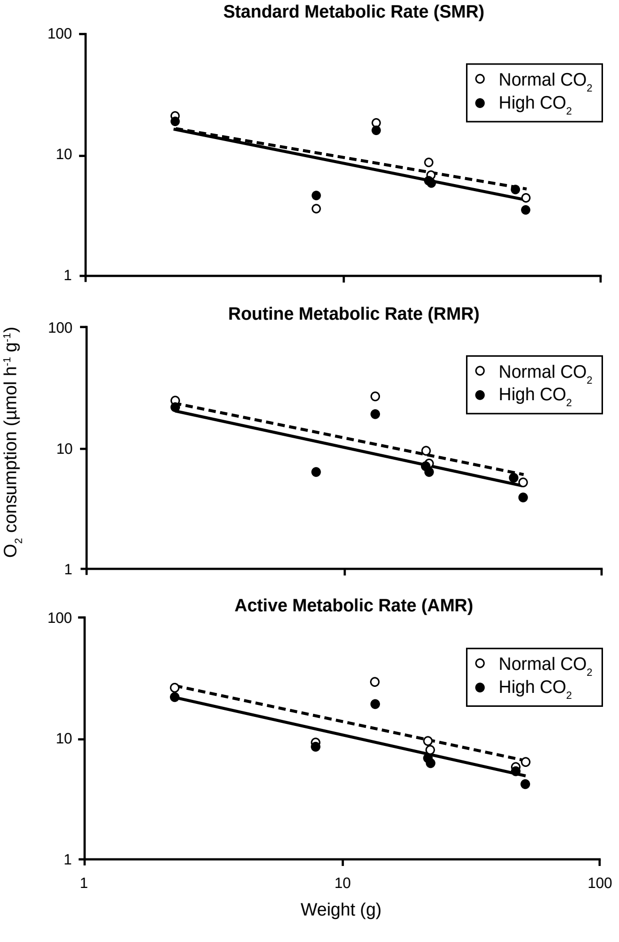

Figure 1. Effect of high CO_2 (0.1%) on standard (SMR), routine (RMR) and active (AMR) metabolic rates of *Dosidicus gigas*.

The lowering of the jumbo squid's metabolism was also evident by the reduction in the number of intervals of elevated activity (as indicated by peaks in oxygen consumption rate) per hour (N_c h^{-1}) and the scope for activity (AMR/SMR) (Fig. 2). This short-term sublethal effect (metabolic depression and reduced scope for activity) may have serious impact on its ability to catch prey and escape predators. Blood oxygen binding experiments in other ommastrephid squid demonstrated lowered blood oxygen binding affinity caused by elevated CO_2 (Pörtner and Reipschläger, 1996) and on-going enzymatic analysis of octopine production may show a premature switch to anaerobic energy production under these conditions.

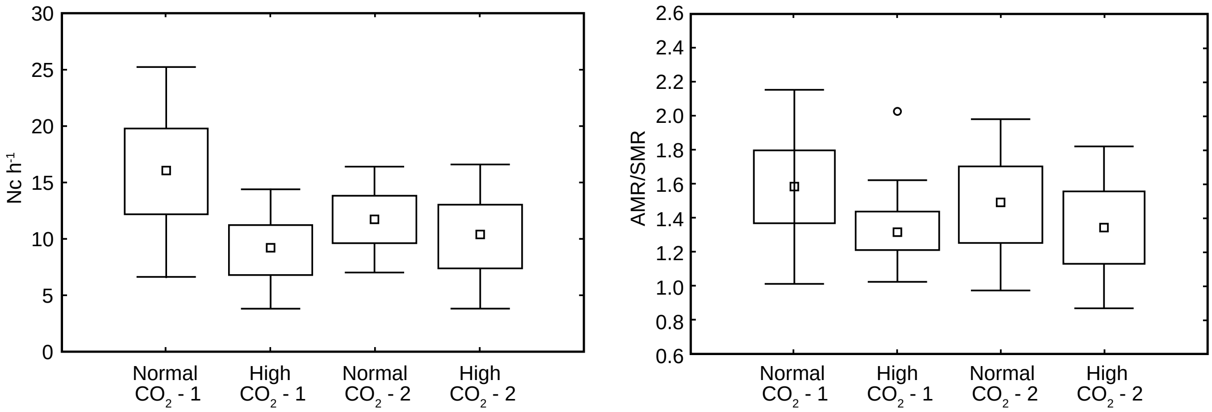

Figure 2. Effect of high CO_2 (0.1%) on the number of active cycles per hour (N_c h^{-1}) and scope for activity (AMR/SMR) of *Dosidicus gigas*.

D. gigas undergoes diurnal migrations, spending the daytime in deep, cold and oxygen-depleted water (oxygen minimum layer - OML; 10°C at around 300 m) and migrates at night to shallow, warm (up to 30°C) and oxygenated surface waters. Under the low oxygen conditions of the OML (only a fraction of a kilopascal) in addition to elevated CO_2 levels (pH drops to 7.5), *D. gigas* may reduce total energy expenditure by shutting down expensive cellular processes (e.g. protein synthesis). Although CO_2 or pH are common triggers of metabolic suppression, our results indicate that slightly elevated CO_2 itself does not cause a substantial metabolic suppression while in the OML.

In conclusion, elevated environmental carbon dioxide and the consequent acidification seemed to interfere with the jumbo squid's respiratory physiology, which may have cascading and long-term impacts on its ecology. While the effects reported here are subtle, much larger impacts are expected in ongoing studies as carbon dioxide exposure coincides with higher temperatures consistent with *D. gigas*' night-time depth distribution.

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Prey size-predator size relationships of squid and their predators in the Northwest Atlantic

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Quantile regression analysis was used to evaluate absolute and relative body size relationships (BSR) between squid and ten predators in the Northwest Atlantic. Minimum (lower bound), median, and maximum (upper bound) slopes were estimated using scatter plots of absolute body lengths. Relative BSRs were compared using trophic niche breadth, defined as the range of relative prey sizes consumed ontogenetically by a predator (Scharf *et al*., 2000). Differences in size-based predation on squid were contrasted with predation on fishes to determine if the two prey resources are functionally similar, as has been previously suggested (Packard, 1972). Predator and prey length data were compiled from the National Marine Fisheries Service long-term ecosystem monitoring programme, the Apex Predators programme of the Massachusetts Division of Marine Fisheries, and from several other independent surveys conducted regionally from 1977 to 2004.

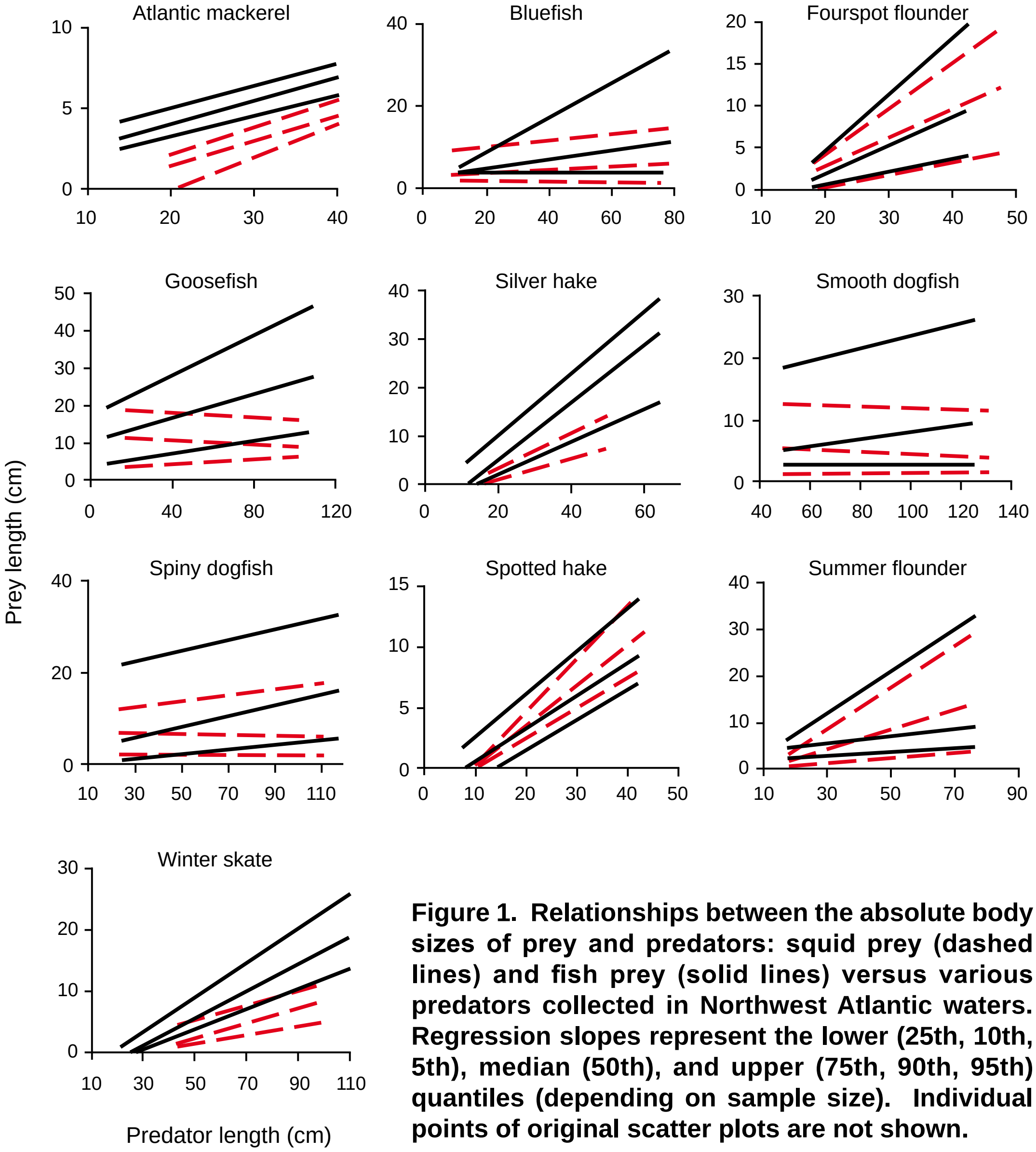

Figure 1. Relationships between the absolute body sizes of prey and predators: squid prey (dashed lines) and fish prey (solid lines) versus various predators collected in Northwest Atlantic waters. Regression slopes represent the lower (25th, 10th, 5th), median (50th), and upper (75th, 90th, 95th) quantiles (depending on sample size). Individual points of original scatter plots are not shown.

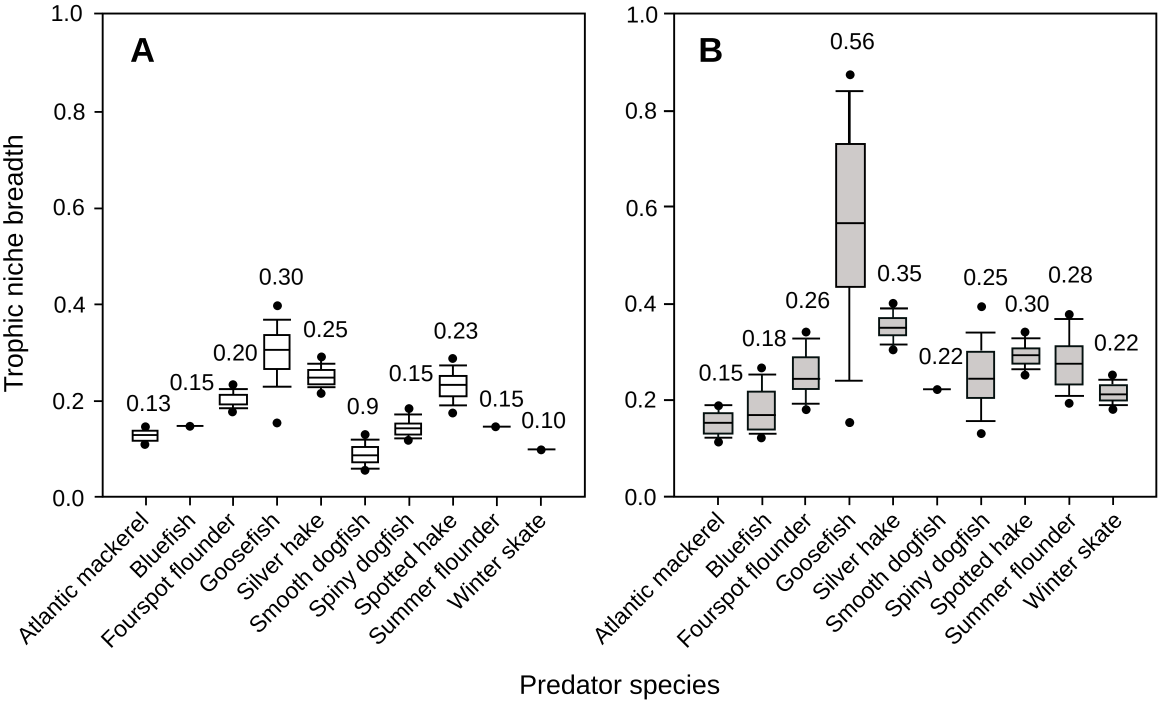

Figure 2. Box plots of relative body size relationships between a) squid b) prey fishes and ten predator species. Noted values indicate mean trophic niche breadth respective to each predator. Box boundaries represent 25th and 75th percentiles, lines within boxes mark the median. Error bars indicate the 90th and 10th percentiles. Circles show outliers in the 5th and 95th percentiles.

Upper and lower bound slopes for absolute squid–predator BSRs ranged from negative (i.e. goosefish) to positive (i.e. fourspot flounder) and spanned orders of magnitude among predators (Fig. 1). Squid slopes were less steep in comparison to prey fish slopes; also, total ranges of squid sizes consumed were smaller than fishes. The majority of predators exhibited expanding ranges of prey fish sizes consumed with increasing predator size (all except Atlantic mackerel, smooth and spiny dogfish). Conversely, when feeding on squid, the majority of predators (all except fourspot flounder, silver hake, and summer flounder) exhibited no change in range with increasing predator size (lower and upper bound slopes were parallel). Evaluation of relative BSRs revealed that squid occupied narrower trophic niche breadths in comparison to prey fishes for all predators (Fig. 2). Results indicate both the upper limit and total range of size-based predation on squid is more moderate in comparison to prey fishes. Gape limitation has often been cited as a limiting factor in size-based predation. However, for the majority of predators analysed here, other factors are clearly influencing predator-prey size relationships. Predators were physically capable of consuming broader ranges of squid sizes evidenced by steeper upper bound slopes and broader trophic niche breadths found respective to prey fishes. A greater number of fish species were included in analyses and likely reflect a greater range of available prey sizes in comparison to squid. Predator–prey behaviour, predator mobility, and habitat overlap are potential factors influencing size-based predation on squid and are responsible for the different patterns in prey resource utilisation seen between squid and fishes.

Loligo pealeii is the cephalopod that is most frequently found in predator diets in the northwest Atlantic, and a highly-valued commercial resource. Consequently, it is important to assess whether fishers are competing with predators for similar squid resources regionally. Lengths of *L. pealeii* recovered from the diets of 31 predators, including marine mammals, finfishes, elasmobranchs and large pelagics, were compared to the lengths of squid harvested by the commercial fishing industry to evaluate the degree of overlap between squid user groups. A Kolmogorov Smirnov test detected significant differences ($D = 0.69$, $p < 0.001$) between the lengths of squid consumed by predators and harvested by the fishery (Predator mode = 4 cm, median = 7 cm; Fishery mode = 12 cm, median = 16 cm).

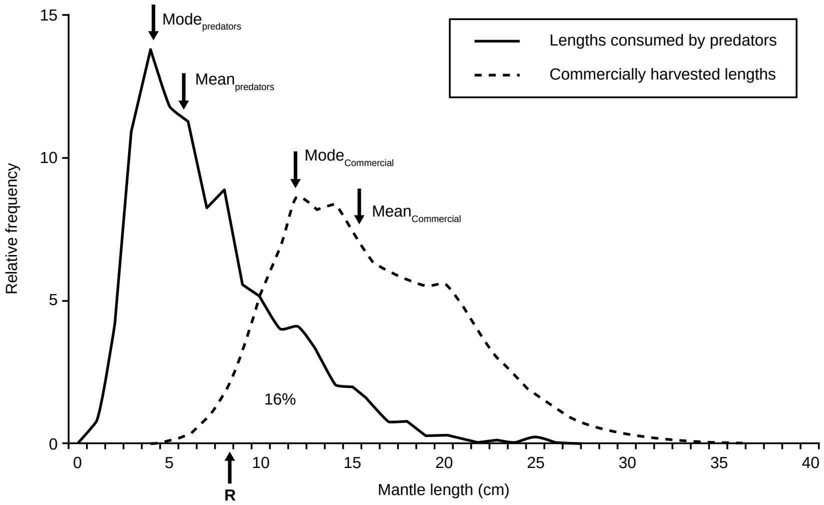

Figure 3. Relative frequencies of mantle lengths of *Loligo pealeii* consumed by 31 predators (solid line) and harvested by the commercial fishing industry (dashed line) in the Northwest Atlantic. The overlapping area under the two curves totalled 16%. Arrows point to the mode and mean mantle lengths of the squid consumed by predators and harvested by commercial fishermen. "R" indicates the size (> 8 cm) at which *L. pealeii* are recruited into the fishery. Commercial data were provided by the National Marine Fisheries Service.

The overlapping area under the two curves (Fig. 3) totalled 16% with the greatest peak at 10 cm mantle length. It appears that predators are targeting smaller squid in comparison to the commercial fishing industry. However, many of the predator stocks included in the above analyses have experienced severe age-truncation over recent decades, and data on the largest individuals are scarce. Therefore, as management efforts seek to recover predator populations and increase biomass in larger size classes, it will be important to monitor how size–based predation changes as a result of shifts in predator population size-structure.

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Comparing squid optimal cost of transport speeds to actual field migrations: new data from 40-g *Loligo opalescens*

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Introduction

We took advantage of an extensive array of over 100 acoustic receivers that are used collaboratively for a variety of projects inside Puget Sound, Washington, to monitor the movements of the California market squid, *Loligo opalescens*. The squid population in the Sound appears to fluctuate strongly, and although squid are abundant during some years, there has not been enough stability to support a significant commercial fishery. Little is known about what these squid are doing there, or how the Puget Sound population might interact with oceanic populations of the same species.

Methods

Between 16 September and 14 December 2005, we tagged 35 squid with 9 mm diameter VEMCO V9 coded acoustic tags, using a custom-designed tool to insert the tags into the small mantle cavity (Fig. 1). The V9 tag has been extensively used for tagging salmon smolts by the Pacific Ocean Shelf Tracking (POST) project (Welch *et al.*, 2003). One squid was tagged in northern Puget Sound; 34 others were tagged from a fishing dock on Vashon Island in the middle of the Sound. The Vashon site was desirable because, if squid were migrating out of the Sound, the tags would be detected by the POST project, which maintains curtains of receivers across the Strait of Juan de Fuca and around Vancouver Island. If the squid were migrating into the Sound, they would be detected by an array of receivers operated by the Squaxin Tribe south of the Tacoma Narrows.

Figure 1. VEMCO V9 coded tag and tool designed to insert tag into mantle cavity.

Results

One third of the 34 squid tagged between 16 September 2005 and 14 December 2005 were detected on at least one of the receivers in the Sound (Table 1 and Fig. 2). The predominant direction of movement was south into the Sound over the entire period. Average rates of travel were significantly higher to the south than to the north (4.0 vs. 2.5 km/d), suggesting directed movement south, independent of tidal currents. There were no detections outside the Sound, even though the average detected tag continued to be detected for nearly two weeks and one was detected after six weeks. The squid were tracked at up to 6.9 cm/s or 6.0 km/d, and at that speed the maximum range could have been up to 300 km, certainly adequate to take them through the POST curtains, to many other receivers in the north, or for them to be detected by a sizeable array in the inner

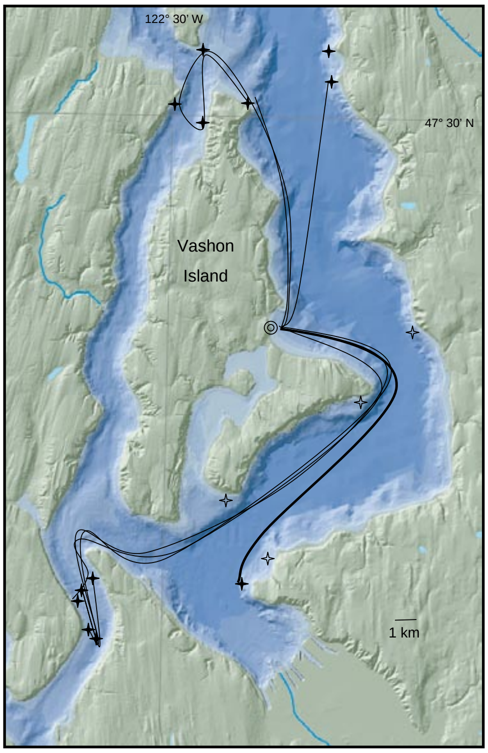

Figure 2. Movements of 10 *Loligo opalescens* in Puget Sound, Washington. All squid, except one further north (See Table 1, Tag 3636), were tagged on Vashon Island (circle) and detected at stationary receivers (stars). The track lines are hand-drawn and represent minimum distances moved. The heavy line shows a route taken by 4 squid. Four receivers (unfilled stars) were removed on 27 September when the season for another project ended, illustrating the need for current efforts to co-ordinate and fund receiver arrays in the region as a permanent, shared multi-user system. The bathymetric map was produced by David Finlayson at the University of Washington, Seattle.

Sound to the south. The tentative conclusion is that the squid are moving deeper into the Sound to breed, as they do in Monterey Bay, California and Bamfield, British Columbia. Alternatively, Puget Sound may have a resident population, but it will take many more tags deployed over more of the season and in more areas to confirm this.

It is exciting to have demonstrated a technology to track such small squid, as this will extend the potential for understanding more of the life cycles and migrations of most commercial species. It is also interesting to extend laboratory-field projections to smaller species. *Loligo opalescens* was the first ever squid to swim in a swim-tunnel respirometer (O'Dor, 1982). Larger swim-tunnels have made it possible to directly measure the cost of transport for a range of larger species, and many of them have also been tracked in nature. Figure 3 illustrates that a fairly wide spectrum of commercial squid species undergo extensive migrations, travelling at optimal rates that are predicted from laboratory studies. This could be of great value for understanding the dynamics of squid life cycles, range expansions, and how they are likely to respond to climate change.

Table 1. Summary of tracked squid

Squid tag no.	Mantle length (cm)	Release (time, date)	Sites (#)	Time (d)	Distance (km)	Heading
3636	12.0	16/09/05 22:45	2	4.86	2.66	S
3634	13.5	26/09/05 00:18	2	5.11	26.39	S
3639	13.0	26/09/05 01:00	1	44.85	17.08	S
3424	14.0	21/10/05 01:47	1	15.82	17.08	S
3693	16.5	23/10/05 22:15	1	3.84	17.08	S
3697	12.0	24/10/05 00:45	4	34.05	23.95	N, S
3691	14.0	26/10/05 23:00	1	4.00	10.83	N
3706	15.0	26/10/05 23:53	1	11.27	11.72	N
3696	14.0	27/10/05 00:28	3	9.84	30.19	S
3705	14.0	27/10/05 01:11	1	8.65	17.08	S
3698	13.0	14/12/05 22:47	3	4.94	32.89	S
Average	13.7			13.39	18.81	
Median	14.0			8.65	17.08	
Maximum	16.5			44.85	32.89	

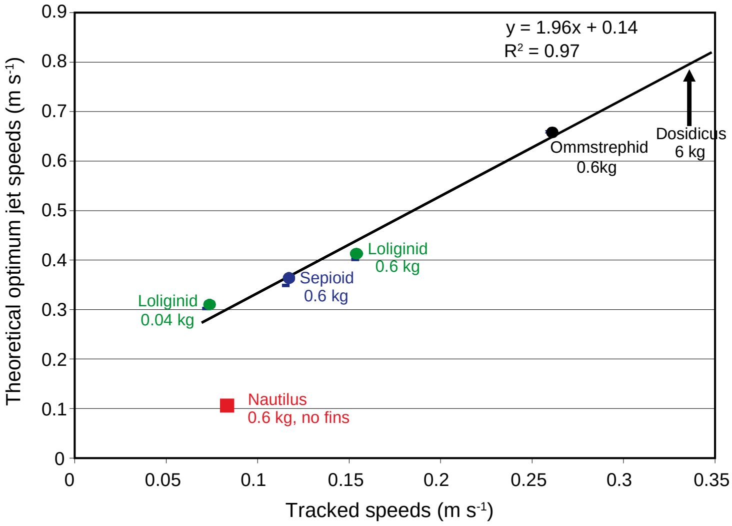

Figure 3. Theoretical optimum speeds that minimise the cost of transport for cephalopods using jets in tunnel respirometers, compared to actual tracked speeds in nature for species with similar anatomies. O'Dor (2002) found that speeds increased as fin size decreased for a series of squid of 0.6 kg mass. Actual maximum tracked speeds are about half of theoretical speeds. The much smaller *Loligo opalescens* tracked here follow the same trend. Tracking speed is shown for much larger *Dosidicus gigas* (Gilly *et al*., 2006), but comparable tunnel respirometry results remain to be completed. The shelled cephalopod, *Nautilus*, which swims purely by jetting, shows better correspondence than the other cephalopods between theoretical and tracked speeds.

Discussion

At the tracked speeds, individual *L. opalescens* and *D. gigas* could undertake migrations on the order of 500 km and 2500 km, respectively, during the last three months of their lives, independent of currents. Taking advantage of currents, some squid have exhibited further increases to this range (O'Dor, 1992). Although we still understand little of how these two species use this mobility, we now have demonstrated the tools necessary to answer the questions. Clearly, these squid could make extensive migrations to find areas of high production for feeding and return to natal spawning grounds. Alternatively, although individual life spans are short, the squid could spawn in new areas with appropriate conditions and expand the species range. This capacity to migrate, combined with rapid growth and high reproductive output, gives squid a formidable capacity to adapt to changing conditions, so we should not be surprised that they are increasing their biomass relative to longer lived vertebrates with less adaptable life styles.

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Fin flaps: key adaptation for habitat expansion in the squid, *Dosidicus gigas*?

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Introduction

The Humbolt squid, *Dosidicus gigas*, appears to have undergone a major range and biomass expansion in recent years. There has been much speculation about whether this has resulted from expansion of suitable habitats as a result of climate change or an increased competitive advantage as a result of decreasing predation or competition associated with declining stocks of large fishes. We suggest here that, regardless of the controlling mechanism(s), *D. gigas* must be remarkably efficient and adaptable in a wide variety of conditions to make range expansion possible, including the ability to utilise the hypoxic mesopelagic environment known as the oxygen minimum layer. Here we describe a previously unrecognised anatomical feature that may provide another mechanism allowing this squid to be a great generalist, rather than a specialist.

Observations

Cephalopods are fundamentally jet propelled, although jets are inherently inefficient because of low Froude efficiency (O'Dor, 1988, 2002). Although jetting achieves high accelerations in order to escape from predators and to attack prey, the modern shell-less coleoid cephalopods nearly all supplement their jets with fins of various sorts. These fins develop from three dimensional muscle cell complexes called muscular hydrostats (Kier *et al*., 1989), producing structures ranging from the fringing fins of neutrally buoyant cuttlefish (Kier *et al*., 1989), to the large and powerful wing-like fins used for soaring in currents by *Loligo* squid (O'Dor *et al*., 1994), to the much smaller fins of climb-and-glide swimming *Illex* (Hoar *et al*., 1994) - both denser than seawater and negatively buoyant. During recent tagging studies in the Sea of Cortez, Mexico, we noted that the fins of *Dosidicus*, otherwise similar in size and shape to those of *Illex*, have extremely thin and flexible hydrostat 'flaps' on the head-ward edge of the fin (Fig. 1), equal to about 10% of the fin area. We

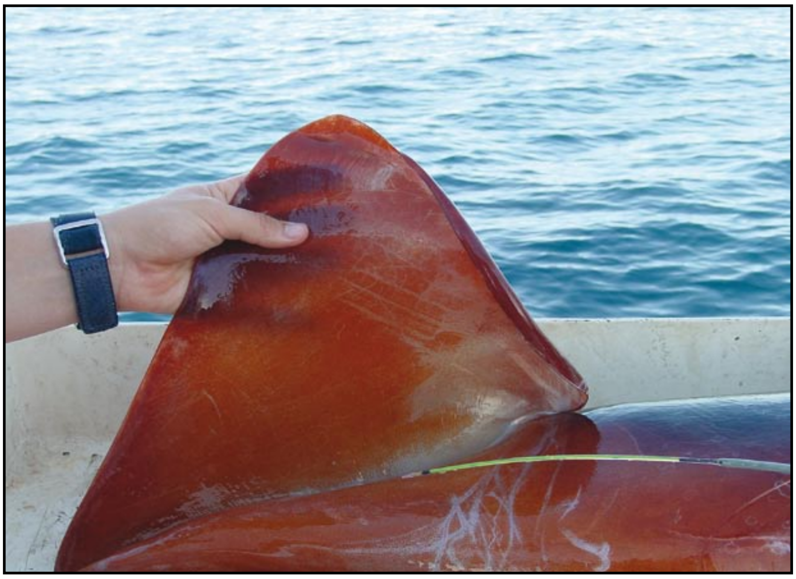

Figure 1. A partially furled fin flap on a living *Dosidicus gigas* of 710 mm mantle length. The watchband is 20 mm wide, for reference.

have since observed the fin flaps in action in a variety of existing images and video footage, but have not yet carried out any quantitative analysis.

Detailed anatomical studies of the fin-flaps are currently underway, and Table 1 indicates that the fin flaps become fully developed only in relatively large specimens. Below about 25 mm mantle length (ML), there is a clear band at the anterior edge of the fin that lacks chromatophores, and it does not obviously look like a flap. It is thinner than the rest of the fin, but is not folded over when preserved in ethanol. In larger specimens above 50 mm ML, this region is folded over in ethanol preserved specimens and is obviously flap-like. The extreme anterior edge also seems to lack chromatophores in the larger specimens.

Table 1. Anatomical measurements (mm) of fin flaps

Dorsal ML (mm)	Fin length	Fin width	Flap width
indistinct			
<25.0	-	-	-
thin			
26.2	7.5	7.1	0.4
29.0	9.0	7.5	0.7
30.5	9.7	8.6	0.5
30.0	13.0	8.5	0.6
distinct			
55.0	19.3	16.5	1.3
50.8	18.2	16.2	1.0
58.0	18.4	17.1	1.3
350.0	?	?	8.0
710.0	318.0	209.0	15.0

Interpretation

Like the flaps and ailerons of airplanes, these squid fin-flaps can alter swimming performance in many ways: steering, braking, increasing lift, reducing drag, and other more complex effects derived from non-fixed-wing functions. When flaps are folded completely, *Dosidicus* fins can function like *Illex* fins, minimising drag during long migrations and increasing efficiency by making long downward horizontal glides (O'Dor, 1988). Tunas, which are also negatively buoyant, use this same mechanism to increase migration efficiency.

The most obvious use of flaps on airplanes is during landing when increasing wing curvature increases lift at low speeds, also a key feature of gliders. Fin-flaps would allow *Dosidicus* to soar in tidal currents around underwater structures like seamounts or canyon walls. These habitats appear to be favoured by this species, and the currents associated with such structures deliver potential prey. Loliginids typically soar with their heads facing into the current, allowing a head-first interception of prey, although it is not uncommon to see squid in the same school facing in opposite directions. *Dosidicus* fin-flaps would seemingly work best for lift if the squid point fin-first into the current. Squid eyes provide a near-360° view, so fin-first orientation would not be a disadvantage for predation. If the flaps are folded flat, they cause only a small fraction of the drag of large loliginid fins, so attacks may be faster allowing them to catch larger, faster prey. *Illex* have been observed to attack larger prey by over-taking them, using faster fin-first jetting, and then dropping back to make a head-first attack (Foyle and O'Dor, 1988), so there are many possibilities. Video observations make it clear that the flaps are also used like ailerons to increase manoeuvrability.

It has also been suggested (Tierney Thys, pers. comm.) that the most critical use of the flaps may be in escaping predators, not catching prey. *Dosidicus* have been filmed flying in air fins first (Cole and Gilbert, 1970), apparently being chased by predators beneath. Increased lift and control in air could be critical to predator avoidance, as in flyingfishes. Maximum speed or acceleration in cephalopods is always achieved by jetting fins-first, and this would be the right orientation for lift. We have re-analysed Gilbert's original footage, provided by the National Geographic Society, but unfortunately the resolution was inadequate to determine what the fin-flaps were doing.

To the best of our knowledge fin-flaps have not been described for other squid, so it is important to look for them in other species. Examination of specimens of *Sthenoteuthis oualaniensis* in our possession reveals the same sort of fin-flap structure. This species is most closely related to *Dosidicus* genetically (our unpublished analysis), but do other ommastrephid species also bear fin-flaps? Knowing that they exist, it is also important to look at what they are doing in a wide range of circumstances. Observations of *Dosidicus* in swim-tunnels are now underway, which should help understand some of the quantitative aspects of fin-flaps. But, footage of them in a variety of natural circumstances is essential to understanding how the flaps are used behaviourally to aid one of the ocean's major predators.

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Acknowledgements

This work is a contribution to the Census of Marine Life.

Epiplanktonic squid from the west coast of the Baja California Peninsula, Mexico

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Cephalopods are the most frequently eaten food items of several top predators caught off Baja California and south to the Gulf of Tehuantepec, in the Gulf of California, and at the Revillagigedo Islands. The most important cephalopod taxa recordered in the stomach contents of sailfish *Istiophorus platypterus*, hammerhead shark *Sphyrna lewini*, yellowfin tuna *Thunnus albacares*, and dolphinfish *Coryphaena hippurus* are: *Dosidicus gigas*, *Abraliopsis affinis*, *Onychoteuthis banksi*, *Gonatus* spp., *Mastigoteuthis*, *Loligo opalescens*, *Thysanoteuthis rhombus*, *Ancistrocheirus lesueuri*, *Sthenoteuthis oualaniensis*, and *Argonauta* spp. (Galván-Magaña, 1988). In spite of the importance of these mollusks in the trophic web, knowledge of the adult cephalopod communities in waters off Mexico is still incomplete.

Identification of squid early stages that live in the plankton is problematic. Through the identification of the paralarvae, a better understanding of the reproductive biology of the adults and their life cycles is attainable. This will help to identify spawning areas and to estimate early growth rates of the target species. The objective of our study was to describe the distribution and abundance of the epipelagic squid collected along the west coast of the Baja California Peninsula, Mexico, during the winter and summer of 1998 and 1999, and to obtain some basic information on the community structure in relation to oceanographic processes.

The biological material was collected during four oceanographic cruises made from Ensenada, BC to Punta Abreojos, BCS, Mexico, during the winter and summer of 1998 and 1999 by the "Investigaciones Mexicanas de la Corriente de California" (IMECOCAL) programme (Fig. 1). All paralarvae were sorted from the plankton samples collected with standard Bongo net tows (Smith and Richardson, 1979), and were identified to the lowest possible taxonomic level, according to the criteria of Roper *et al*. (1984) and Sweeney *et al*. (1992). Abundance data were standardised based on Kramer *et al*. (1972). Taxa were grouped by biogeographic affinity of the adults (Roper *et al*., 1984).

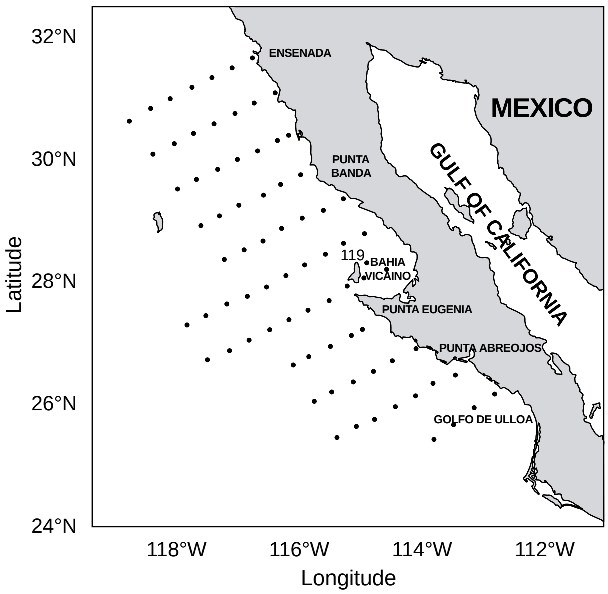

Figure 1. Study area and grid sampling stations.

Squid paralarvae were collected at 122 of the 268 IMECOCAL sampling stations. The specimens were grouped in 8 families, 12 genera, and 29 other taxa. Total squid paralarvae (PL) abundance in the four cruises was 917 PL/1000m^3. Three families were the most important, accounting for 84% of the relative abundance of the paralarvae recorded during the four cruises. Paralarvae of the family Onychoteuthidae were the most important, representing 33% of the total abundance, followed by the Cranchiidae (28%), and the Gonatidae (23%). Important differences in PL abundance and number of taxa were found among the 1998 and 1999 cruises. Six more species of the family Ommastrephidae, were previously identified from the 1998 cruises (Camarillo-Coop, 2006), resulting in a total of 35 epiplanktonic squid taxa in the study area.

Durazo and Baumgartner (2002) mentioned that the signal of the *El Niño* event of 1998 reached its maximum expansion along the west coast of the Baja California Peninsula in July 1997, with unusually warm and salty water. The winter of 1998 was considered a transition period between *El Niño* and *La Niña* events. During October 1998 (summer), negative sea surface temperature anomalies established the presence of a *La Niña* event, which was recorded until August 1999 in our study area.

During the winter of 1998, we recorded the paralarvae of temperate, cosmopolitan, and tropical taxa associated to the subarctic and transitional-subtropical water masses along the Baja Peninsula (Fig. 2). During summer 1998, the taxa of cosmopolitan and tropical affinities were less abundant, with taxa of tropical affinity distributed only in the southern, warmer region of our study area. The major presence of subarctic water in these months resulted in an increase of the temperate taxa. During the winter of 1999, we identified 5 taxa, all of temperate affinity, while in summer 1999, at the end of the *La Niña*, temperate taxa were dominant but cosmopolitan taxa increased again.

In the study area, the affinity of squid PL to water masses has been previously established. Paralarvae of *Dosidicus gigas* were the most abundant during the 1997-1998 IMECOCAL cruises, followed by those of *S. oualaniensis*, and the S-D group, which represents spawning events of the mentioned species. These species were associated with the transitional-subtropical water mass, while the temperate species *Eucleoteuthis luminosa* and *Hyaloteuthis pelagica* were associated with the subarctic water mass. The S-D group represented spawning events of the first two species (Camarillo-Coop, 2006).

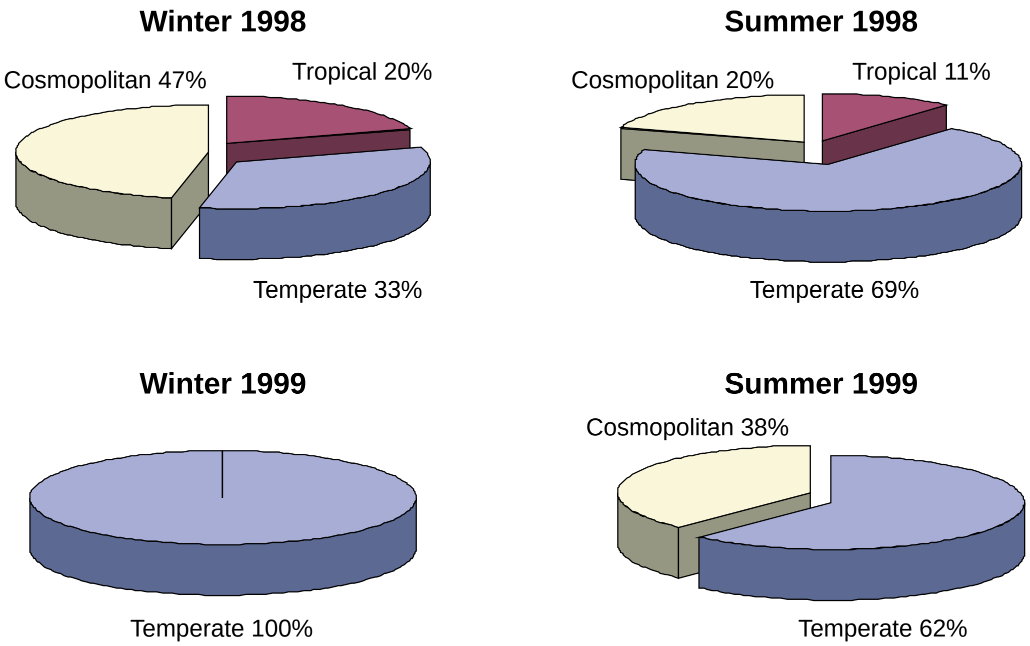

Figure 2. Relative abundance of squid paralarvae by adult affinity during the winter and summer of 1998 and 1999.

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Post-spawning egg-care in the squid, *Gonatus onyx*: implications for diving mammals

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Gonatus is among the most abundant cephalopod genera in the upper layers of the subarctic Pacific and Atlantic Oceans, and falls prey to a variety of birds, fishes and mammals. The bottlenose whale, *Hyperoodon ampullatus*, for example, is known to feed primarily on *Gonatus fabricii* and efforts are underway to extend protection of the whale by including squid life history parameters among conservation priorities. However, the life history of gonatid squid is unresolved, in part because of the paucity of scientific observations at the great depths where spawning is believed to occur. All known squid species die after spawning, leaving the eggs to develop on their own. Here we report direct observations of post-spawning parental egg-care (i.e. brooding) in the squid, *Gonatus onyx* (Fig. 1). *G. onyx* were observed between 1500 and 2600 metres depth holding an egg mass in their arms. They ventilated the egg mass and provided protection from predators via active locomotion. Upon extended pursuit they mechanically agitated the egg mass, triggering premature hatching.

Figure 1. A female *Gonatus onyx* brooding an egg mass photographed at 1590 metres depth in Monterey Canyon, as observed by the ROV Tiburon, Monterey Bay Aquarium Research Institute.

Gonatus onyx in the California Current, and *G. fabricii* in the North Atlantic, are both known to undertake an ontogenetic descent to great depths where spawning is believed to occur. Initially, researchers concluded that the eggs must be deposited on the seafloor and left to develop on their own. More recently, however, Seibel *et al*. (2000) suggested a pelagic egg-brooding behaviour for *G. onyx* based on indirect evidence, including two mature female squid captured in trawls with dissociated eggs at differing stages of development. Although limited evidence also suggests egg-brooding in other gonatid squid, the idea has remained controversial in the absence of direct observations because some aspects of gonatid life history appeared to run counter to the egg-brooding hypothesis. Most importantly, degeneration of the musculature that occurs at some point following sexual maturation was presumed to render the squid unfit for active locomotion and egg protection. However, the present behavioural observations revealed substantial locomotory capacity which degenerates gradually over the entire duration of the egg development period.

Temperature and egg size are the primary determinants of developmental rate in cephalopods. Published equations suggest that *G. onyx* eggs should develop within 3 to 4 months. However, this estimate depends on extrapolation outside the range of sizes and temperatures for which cephalopod development is known, and substantial deviations from predicted values have been documented. The abundance of juveniles of *G. onyx* in near-surface waters peaks seasonally from

April through July, suggesting the possibility of a yearly cycle with an egg-development period lasting as long as 6 to 9 months. This estimate is roughly consistent with the present egg collection dates and the relative developmental progress observed, however much more data is required to clearly demonstrate seasonality. Gonatid squid have large lipid stores in the digestive gland sufficient to fuel metabolism for a long brooding period. The specimen with undeveloped eggs (437) had a firm digestive gland, while those with well-developed embryos appeared to be more flaccid. However, two specimens captured within days of each other carried embryos at apparently different developmental stages, so development is apparently not well synchronised. Seasonality of spawning appears to be more synchronous in *G. fabricii* populations in the North Atlantic.

Juvenile squid were triggered to hatch when pursued persistently by the submersible, presumably a last-resort “escape-hatch” that allows release of potentially viable offspring before they are consumed by a persistent predator. Such behaviour would not be beneficial unless the embryos were able to reach the abundant food supply near the surface, surviving to reproduce. Hatchlings from specimen number 239 survived for as long as 6 weeks in the laboratory without external food sources. These hatchlings appeared to have an extensive internal lipid store that diminished throughout development in the laboratory. These data argue that embryos could hatch at depth and survive to reach the surface, provided that swimming capacity had developed sufficiently at the time of hatching. However, senescent gonatid squid have also been observed at the surface, including one unidentified squid that was releasing hatchlings.

The present observations clearly demonstrate active post-spawning egg care by *G. onyx*. Similar life-history strategies are suspected in other gonatids, as well as other families. Predator avoidance is accomplished by active fin beats and jet propulsion via mantle contractions, which appear to decline in intensity as muscle degeneration progresses. Despite retaining some capacity for escape locomotion, the relatively immobile brooding squid at depth may be a major food supply for larger deep-sea predators, including some fishes. More importantly, beak analysis and fatty acid signatures indicate that gonatid squid are a dominant component in the diets of some whales and elephant seals. The upper depth limit of our observations is within the routine diving range of such predators. Thus, brooding squid may provide an easy target for “mesopelagic mammals” and a direct link between deep and shallow biomes.

These findings are published (Seibel *et al*., 2000, 2005) and additional relevant literature is listed below.

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CLIMATE IMPACTS

How climate change may influence loliginid squid populations

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By the end of the next century, global mean sea surface temperatures (SSTs) are expected to rise substantially (e.g. 1.4 to 5.8°C; Schneider, 2001). However, climate change may mean more than just temperature rises. Other predictions with potential impacts on squid populations include an increase in extreme events, with more intense *El Niño* events and more common *El Niño* like conditions (Easterling *et al*., 2000). Rises in atmospheric CO_2 are also expected, which will cause an increase in surface ocean CO_2 concentrations and result in an estimated drop in pH of about 0.4 units, which may inhibit oxygen uptake by squid (Seibel and Fabry, 2003). Abiotic changes in the world's oceans will also result in concomitant changes in the biotic components. Global warming is expected to increase thermal stratification of the upper ocean, thereby reducing the upwelling of nutrients and decreasing productivity (Seibel and Fabry, 2003). Indeed, the warming of some oceans has already been accompanied by a 70% decline in zooplankton abundance (Roemmich and McGowan, 1995). Loliginid squid populations inhabit nearshore waters and often reproduce in very shallow benthic habitats. Loliginid squid populations are, therefore, likely to be especially sensitive to global climate change and increases in seawater temperatures.

Embryos and hatchlings

As temperatures increase, development times of cephalopod eggs decrease (Boletzky, 1994), provided that temperatures do not fall outside thermal tolerance boundaries (Gowland *et al*., 2002). However, hatchlings emerge quicker under elevated temperatures and there is a negative relationship between incubation temperature and hatchling size (Vidal *et al*., 2002), so that under warmer temperatures loliginid hatchlings will emerge smaller.

Within a single spawning season, Australian southern calamary (*Sepioteuthis australis*) hatchlings, which emerge at the start of the season (cooler), may be as large as 0.057g, whilst at the end of the spawning season (warmer), hatchlings may be as small as 0.023 g – only 40% of the size of the hatchlings at cooler temperatures (Pecl *et al*., 2004a). Warming oceans may, therefore, result in a downward shift in the size of squid hatchlings emerging from inshore spawning grounds, unless females compensate by producing larger and fewer eggs.

Since growth in juvenile cephalopods is exponential, growth works like compound interest on an investment, and the starting size of the investment is crucial (Fig. 1). For example, a 0.023-g hatchling growing at 10% body weight per day would be 186 g after three months, whereas a 0.057 g hatchling growing at the same rate would be 462 g after the same time period. If elevated temperatures reduced hatchling size to say, 0.01 g, a hatchling of this size growing at 10% would only be 81 g after three months.

Adult phase and reproduction

Growth rates of squid are generally linked with temperature, with an increase in temperature leading to increased growth rate (Forsythe, 2004). However, as species approach their physiological maximum temperature, increasing temperatures may become metabolically costly. Also, some species that grow slower in warmer waters may be at their physiological limits with respect to temperature, resulting in reduced growth rates (e.g. *Loliolus noctiluca*; Jackson and Moltschaniwskyj, 2001).

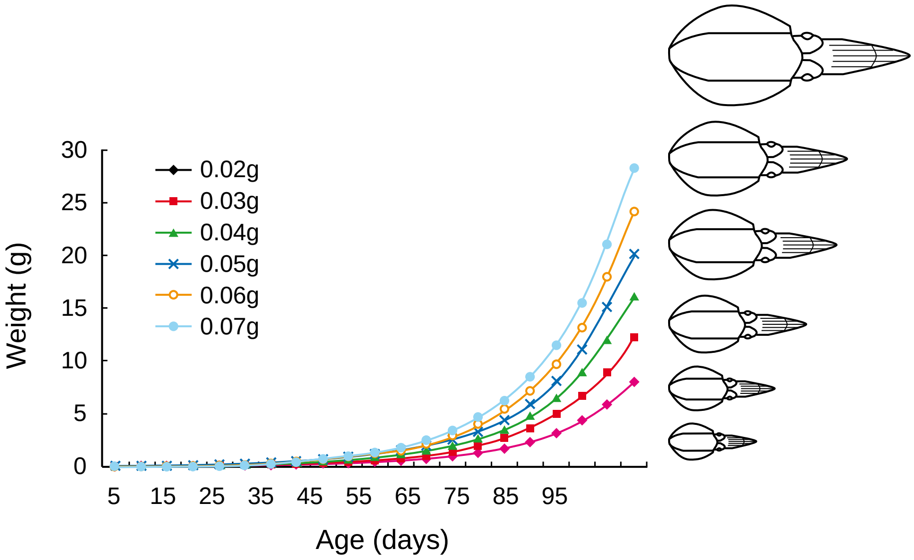

Figure 1. Hypothetical growth curves representing differential growth of *Sepioteuthis australis* that hatched at different sizes and grew exponentially at 6% per day for 100 d.

With respect to potential changes in loliginid growth rates under a regime of elevated temperatures, several outcomes (not mutually exclusive) are possible. Firstly, if individuals are able to obtain sufficient resources of both food and oxygen, see below, growth rates will increase (particularly for males) as will variance in growth rate because, although warmer years may give rise to faster growing squid, slow growers may still be present (Hatfield, 2000; Pecl *et al*., 2004b). However, adult size may not necessarily increase as hatchling size, the starting point, will decrease. Under continued temperature elevation, there will likely come a point where growth rates start to decrease as metabolic costs continue to escalate, and growth potential is subsequently reduced. Secondly, as a function of increased growth rate, it is very likely that the average life-span of squid will decrease (e.g. *L. noctiluca*; Jackson and Moltschaniwskyj, 2001), and individuals will mature younger and at a smaller size (e.g. *Sepioteuthis lessoniana*; Jackson and Moltschaniwskyj, 2002). From field-collected data (Pecl, 2000; Jackson and Moltschaniwskyj, 2002), we know that individuals that grow through cool conditions will have larger gonads and greater reproductive output compared to their warm water counterparts that have shorter life spans and mature at a smaller size. Warm-water squid will have a greater relative gonad investment, with a higher percentage of their body weight as reproductive tissue. However, in absolute terms, their gonads will weigh less.

Energetics

Given the rapid digestion rates of squid, and a protein based metabolism that converts food into growth rather than storage, we can expect that, with increasing temperature, there will be a concomitant increase in feeding rates. The increased temperatures will also result in smaller hatchlings and a decrease in time that hatchlings can survive without food. Thus, hatchlings will need more food but will have less time for finding it before facing mortality. Furthermore, increased levels of CO_2, resulting in decreased ocean pH, might impair O_2 transport in squid. This could ultimately limit scope for activity in squid (Seibel and Fabry, 2003).

Population considerations

General predictions of the effect of global warming on marine populations include: extension of species geographic range boundaries towards the poles, extinction of local populations along range boundaries, and increasing invasion of weedy and/or highly mobile species, especially where local populations of other species are declining (Hughes, 2000). All these features are likely to be observed in squid populations, especially as squid have been referred to as ‘weeds of the sea’ (Jackson and O’Dor, 2001). Moreover, squid biomass may be affected by the carrying capacity of the changing ecosystem. If productivity decreases, however, the rate of cannibalism within squid populations may increase, which ultimately may reduce biomass if cannibalism levels are high.

In conclusion, the next 100 years will see over 100 generations of these highly responsive creatures, in comparison to a handful of generations of sharks, tunas, and other larger predators of our oceans. Squid, and cephalopods in general, have the intrinsic flexibility to adapt to climate change - their life-history and physiological traits enable them to be opportunists in variable environments (Rodhouse and Nigmatullin, 1996). Additionally, we will not have to wait decades to determine what these effects are. In species for which we have established good baseline data, changes will be immediately obvious, generation by generation, year by year. In contrast, for longer-lived predators it will take decades to establish cause and effect on their life-histories, populations and abundance. Whilst definite answers to our questions about ocean-scale climate change and the potential impacts on inshore squid population dynamics or fisheries biology are impossible, one thing is for certain, and that is, should the oceans warm, the pace of life for this high-speed group will increase even further.

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Long-term changes in the stock abundance of neon flying squid, *Ommastrephes bartramii*, in relation to climate change, the squid fishery, and interspecies interactions in the north Pacific

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Introduction

The neon flying squid (*Ommastrephes bartramii*) is an oceanic squid that occurs worldwide in subtropical and temperate waters. In the North Pacific, this species plays an important role in the pelagic ecosystem and is an international fishery resource with high commercial value. We examined the interannual variation in the stock abundance of the autumn spawning cohort of this species, which was monitored initially by Hokkaido University (1979–1999) and recently by the National Research Institute of Far Seas Fisheries (2001-2006), using research driftnets (Yatsu *et al*., 2000; Ichii *et al*., 2006), to understand the effect of climate change, the effect of the large-scale squid driftnet fishery and the effect of interspecific interactions on the squid stock.

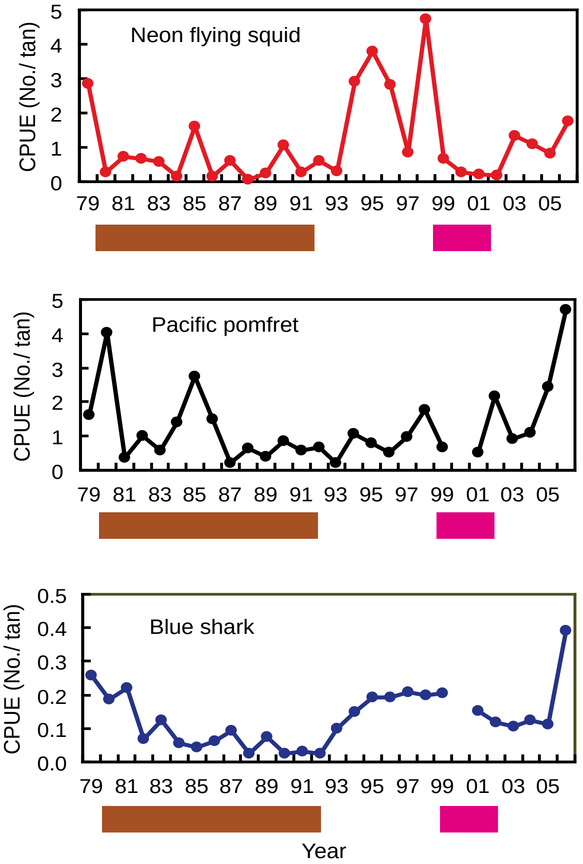

Figure 1. Interannual variation in stocks of the autumn cohort of neon flying squid, large Pacific pomfret, and juvenile blue shark in the North Pacific based on research driftnet catch per unit effort (CPUE, number/tan). Data were obtained by Hokkaido University until 1999 and by the National Research Institute of Far Seas Fisheries from 2001 onward.

Effects of climate change

During the period of 1999-2002, climate change, characterised by a northward displacement of the Aleutian Low and a northward shift of the transition zone chlorophyll front (TZCF), occurred (Bograd *et al*., 2004). This implies a reduced level of primary production in the subtropical frontal zone (STFZ), which corresponds to the spawning ground of the autumn cohort of neon flying squid (Ichii *et al*., 2004). Correspondingly, we found a lower stock level of the autumn cohort during this period (Fig. 1, period indicated by a pink bar). To understand how the lower stock level may be associated with the climate shift, we compared the extent of the productive autumn spawning ground during the productive STFZ regime (1978-1998) to that of the less productive STFZ regime (1999-2002). A temporal and spatial reduction in the extent of the productive spawning ground was observed during the latter regime. When the southern extent of the TZCF was weak (i.e. the TZCF was not observed south of 31°N) in winter, the stock level of the autumn cohort was very low. Thus, interannual variation in the position of the TZCF may have important implications for the stock level of the autumn cohort.

Effects of the squid driftnet fishery

The stock level of the autumn cohort was low during the period of the large-scale driftnet fishery (1980-1998; Fig.1, period indicated by a brown bar). We assessed whether the stock was adversely affected by this fishery (Ichii *et al*., 2006). The relative fishing mortality (F/FMSY) derived from the production model was 0.8-1.2, which was close to the appropriate (maximum sustainable yield, MSY) fishing level of 1.0, even during 1987-1990, when catches were large. The proportional escapement (number of squid alive at the end of the fishing season as a proportion of those that would have been alive had there been no fishing) was 18-64%, with an average of 42%, which was close to the management target of 40%, even during this period. Thus, the large-scale driftnet fishery is considered to have been sustainable.

Effects of interspecific interactions

The squid driftnet fishery also reduced the stocks of Pacific pomfret (*Brama japonica*) and blue shark (*Prionace glauca*) because they were commonly caught in association with neon flying squid. We compared interannual variation in stocks of the autumn squid cohort, large Pacific pomfret, and juvenile blue shark based on the research driftnet data (Fig. 1). After the end of the fishery, the single-aged cohort of neon flying squid increased sharply. Regarding multi-aged species, blue shark stocks increased promptly, whereas Pacific pomfret stocks increased very slowly, even though the latter was more short-lived than the former. Considering that the autumn squid cohort and Pacific pomfret compete with each other ecologically, and they are both the predominant nekton species in the North Pacific ecosystem, it is possible that the autumn squid cohort occupied a trophic niche left unoccupied by the depletion of the Pacific pomfret stocks after the end of the fishery, and hence Pacific pomfret had difficulty reclaiming its former niche.

Concluding remarks

The autumn cohort of neon flying squid was found to respond quickly to environmental and ecosystem changes caused by climate changes and the large-scale fishery, and may have affected ecologically related species.

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How climate change might impact squid populations and the ecosystems: A case study of the Japanese common squid, *Todarodes pacificus*

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Annual catches of Japanese common squid, *Todarodes pacificus*, decreased during the cool regime period from the late-1970s to late-1980s, while Japanese sardine, *Sardinopsis japonicus*, increased exponentially. Squid catch has recently increased after the late-1980s warm regime period. These catch fluctuations are similar with those of Jack mackerel, *Trachurus japonicus*, and the Japanese anchovy, *Engraulis japonicus*. After 1989, the feeding area of the winter spawning stock of squid expanded to the Oyashio region during summer-autumn. These squid feed on small fish and large zooplankton. It has also been suggested that they feed on juvenile walleye pollock, *Theragra chalcogramma*, on the Oyashio shelf region during autumn, and might strongly affect pollock recruitment.

Todarodes pacificus produces gelatinous, nearly neutrally buoyant egg masses that contain many small eggs. These egg masses are thought to occur within or above the pycnocline at temperatures suitable for egg development. Recently, we estimated from laboratory studies that hatchlings (<1mm ML) will ascend to the surface at temperatures between 18-24°C, especially between 19.5-23°C. After hatching, the paralarvae presumably ascend from the mid layer near the pycnocline to the surface layer above the continental shelf and slope, and are transferred into convergent frontal zones.

We used this new reproductive hypothesis to explain the last bi-decadal stock fluctuation related to climatic regime shifts (Fig. 1). During the warm regime period after 1989, the inferred spawning areas of the winter spawning group have occurred along the continental edge off the Kyushu Island

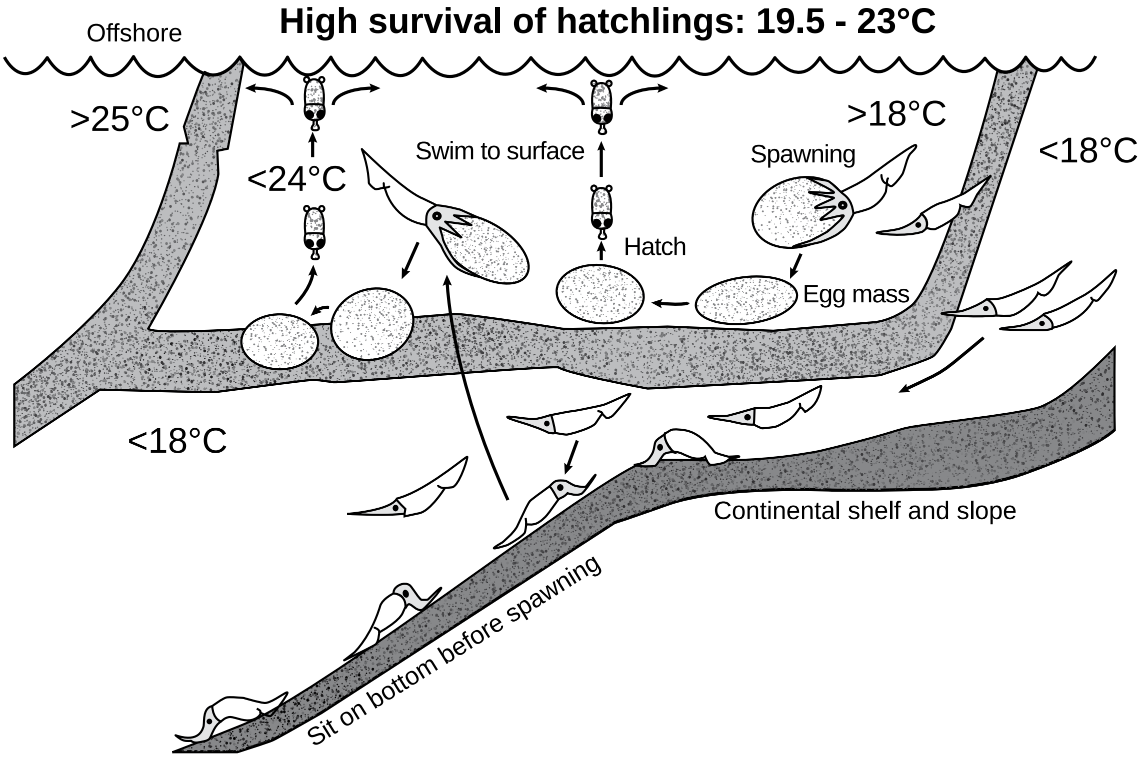

Figure 1. New schematic view of reproductive processes of Japanese common squid, *Todarodes pacificus* (modified from Sakurai *et al.*, 2000).

and the Nansei Islands, and the inner flow of the Kuroshio has transported the hatchlings in the surface layer northeastward along the continental edge from the spawning areas to the nursery areas. However, during the cool regime of the 1980s, when winter wind stress was stronger, air temperature at the sea surface was lower, and mixed layer depth at the spawning grounds was deeper than after 1989, the spawning areas were not connected along the continental edge.

We conclude that short- and long-term change of the *T. pacificus* stock can be explained and predicted by physical parameters such as wind stress, air temperature, SST, and MLD during the spawning period based on this new reproductive hypothesis. Although we cannot forecast climate change, even in the next month or season, we can map the inferred spawning grounds using the SST areas between 18-24°C, especially between 19.5-23°C and within a specific range of bottom topography (100-500 m depth).

Based on this method, we can then monitor the trend of stock fluctuation and structural change, such as a seasonal shift of the spawning period related to abrupt changes of the inferred spawning areas. As an example, we present how to monitor the recent seasonal changes of inferred spawning areas and predict the stock condition of the next year's cohort. Furthermore, we try to predict whether the squid will be extinct or will occupy a marine ecosystem during the 21st century based on the Global Warning Scenario (IPCC, International Panel of Climate Change) using the Earth Simulation System (FRCGC, Frontier Research Center of Global Change, Japan). If we examine the monthly changes of squid distribution (temperature range of distribution: 12-23°C at 50 m depth) and inferred spawning areas in 2005, 2050, and 2099, the northern limit of the squid distribution shifts to the north by 1°/50 yr, and covers the water around Hokkaido Island by 2099. The inferred main spawning grounds also move from the southern Japan Sea and the East China Sea around Tsushima Strait to the East China Sea by 2099. The peak of inferred spawning period shifts from October-February in 2005 to November-March in 2050 and December-April in 2099.

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Studies of the jumbo squid (*Dosidicus gigas* d´Orbigny, 1835) in Mexico: Fishery, ecology and climate

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Introduction

In 2006, the jumbo squid fishery was one of the five principal fisheries in Mexico. Based on 13 years of continuous official records, the jumbo squid is fished mostly inside the Gulf of California, while during ENSO events catches have been recorded off the western coast of the Baja California (BC) peninsula.

The fishery

By analysing the annual landings (Fig. 1), it is possible to reconstruct the history of the fishery. It began as a local artisanal fishery at the beginning of the 1970s. The “artisanal period” was characterised by four years of landings (2000 tonnes) by the artisanal fleet, small boats with outboard motors that operated during the summer from ports in Santa Rosalía and Loreto, Baja California Sur (BCS).

After the federal government negotiated with Asian countries, large companies incorporated squid boats with the technology and capacity to process squid on board (Klett-Traulsen, 1981). This influx of specialised boats began in February 1980 and culminated in November of the same year with landings of 22,464 t of jumbo squid. In 1981, the catches declined by one-half (11,000 t), and the fishery collapsed in 1982 (Klett-Traulsen, 1996). After seven years of no jumbo squid landings in Mexico, small catches were recorded in 1989 in the state of Sonora, coinciding with a *La Niña* event (Schwing *et al*., 2001). Starting in 1990 and lasting until 1993, the Gulf of California experienced a period of anomalous warm SSTs caused by *El Niño* conditions (US NOAA Climate Prediction Center website, http://www.cpc.noaa.gov/). During these years, the National Fishery Institute conducted exploratory fishing for jumbo squid, and found important quantities on the western coast of the BC peninsula, and 6,500 t were landed in the port of Ensenada BC. The following period in the fishery began in 1994 and has lasted 13 years. Korean companies began operating in the ports of Guaymas, Sonora; Santa Rosalía and Loreto, BCS; and La Reforma, Sinaloa. The Mexican government permitted the installation of foreign-owned processors, but limited catches by Mexicans, and authorised the operation of pangas and shrimp boats adapted for fishing jumbo squid. The landings reached an historical maximum of 117,351 t in 1997, followed closely in 2002. During the 13 years of this stage, the price paid to the fishermen on the beach

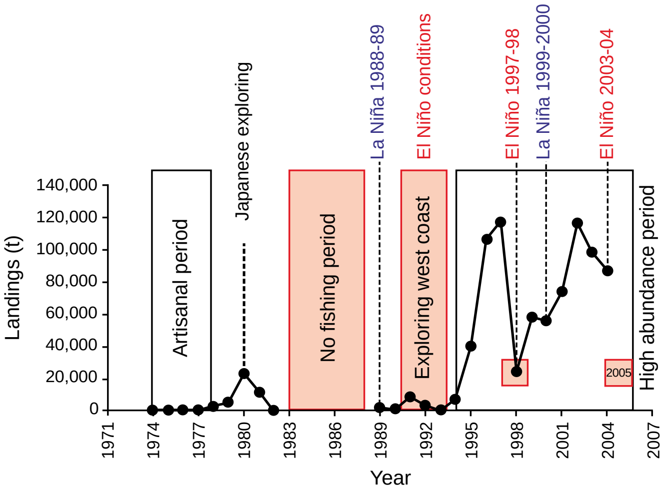


Figure 1. Historical record of jumbo squid landings in Mexico.

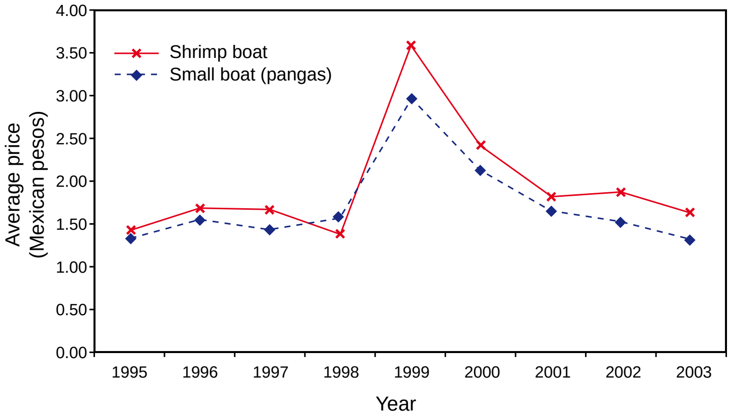


Figure 2. Annual variations in the beach price of jumbo squid in Guaymas, Sonora, Mexico.

increased, then declined (Fig. 2), causing discontent and demotivation. Most of the Mexican squid production is exported as daruma to Korea and Japan, a small amount goes fresh-frozen to the United States, and a smaller amount is exported fresh-frozen to Spain. In the national market, jumbo squid is sold fresh-frozen, as frozen fins and tentacles, and recently as breaded and dried fillets. The public consumption of jumbo squid in the northwest of Mexico increased by 36% from 2003 to May 2006.

Ecology

Given the socioeconomic importance of the jumbo squid fishery in Mexico, it is necessary to increase our knowledge of this species to improve its sustainable management. In 2003, the Jumbo Squid Team of CIBNOR began surveying the population off the west coast of the BC peninsula to describe its ecological role in the pelagic ecosystem inside and outside of the Gulf of California, to determine the diagnostic morphogenetic characteristics of the paralarvae, and to better understand the characteristics of its habitat in Mexican waters and the reason for its latitudinal expansion. One of the first results of these investigations is a historical time series of the size composition of the landings (Fig. 3; Bazzino *et al*., submitted). Changes in the size structure of the population during 1995-1997 and 1998-1999 suggest that the occurrence of the 1997-1998 *El Niño* not only affected the abundance of jumbo squid inside the Gulf of California (Lluch-Cota *et al*., 1999), but also affected the population structure (Markaida, 2006). Our results indicate strong variability in the population structure inside the Gulf of California, based mainly on the size structure and length of first maturity. Variability in jumbo squid abundance and population structure seems to be related to the occurrence and intensity of ENSO events.

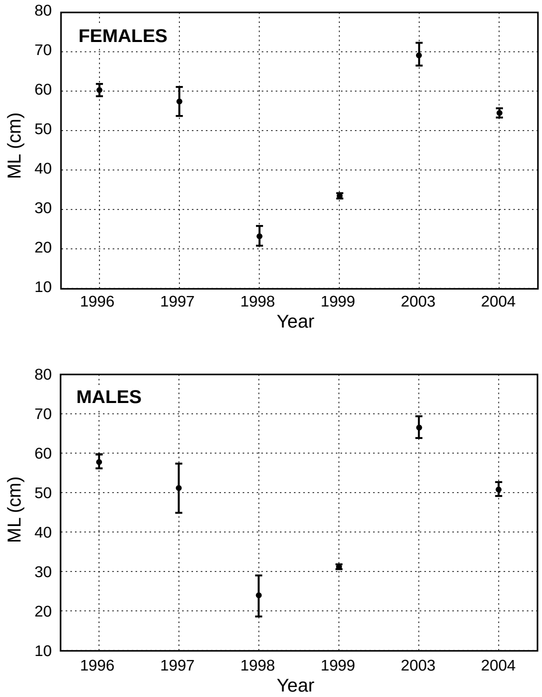


Figure 3. Average mantle length of jumbo squid landed in Santa Rosalía, BCS, Mexico.

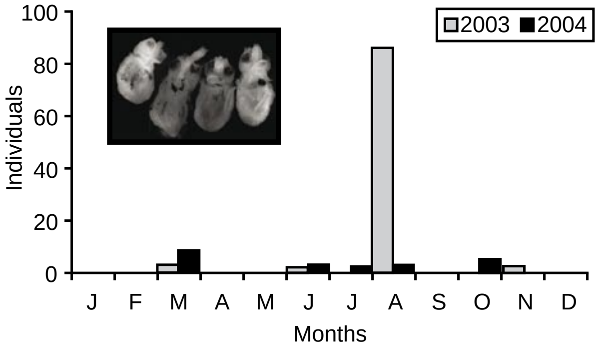
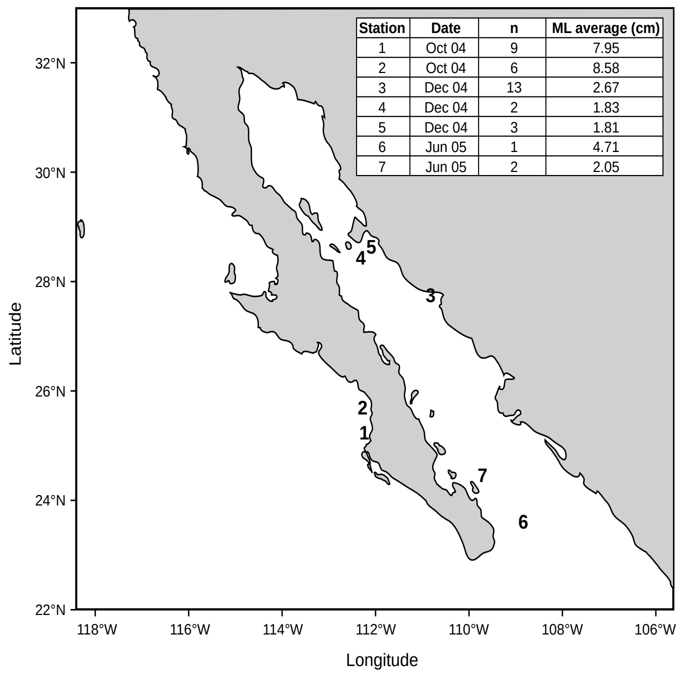


Figure 4. Numbers of ommastrephid paralarvae (inset) caught off Santa Rosalía, BCS, Mexico by month during 2003 and 2004.



Station	Date	n	ML average (cm)
1	Oct 04	9	7.95
2	Oct 04	6	8.58
3	Dec 04	13	2.67
4	Dec 04	2	1.83
5	Dec 04	3	1.81
6	Jun 05	1	4.71
7	Jun 05	2	2.05

Figure 5. Sites in Mexico where juvenile *Dosidicus gigas* were collected.

Presence of paralarvae and juveniles in the Gulf of California

During 2003 and 2004, we made nocturnal surface hauls with a 60 cm diameter, 505 µm conical net, and collected *Rhynchoteuthion* paralarvae characteristic of the family Ommastrephidae (Fig. 4). This indicates presumably that *Dosidicus gigas* spawns in this area.

In research cruises inside and outside the Gulf of California, juvenile squid between 1.81-8.58 cm mantle dorsal length (MDL) (Fig. 5) have been collected, which suggests a wide distribution of spawning and nursery grounds. These organisms were preserved in alcohol for future genetic analyses.

Presence of paralarvae and adults off the west coast off Baja California

Since 2004, we participated in collecting jumbo squid off the west coast of the BC peninsula, and jumbo squid were caught at all stations during all cruises. In 2005, one side of the bongo net was preserved in ethanol for studies of the morphogenetic identification of *Rhynchoteuthion* paralarvae (Fig 6).

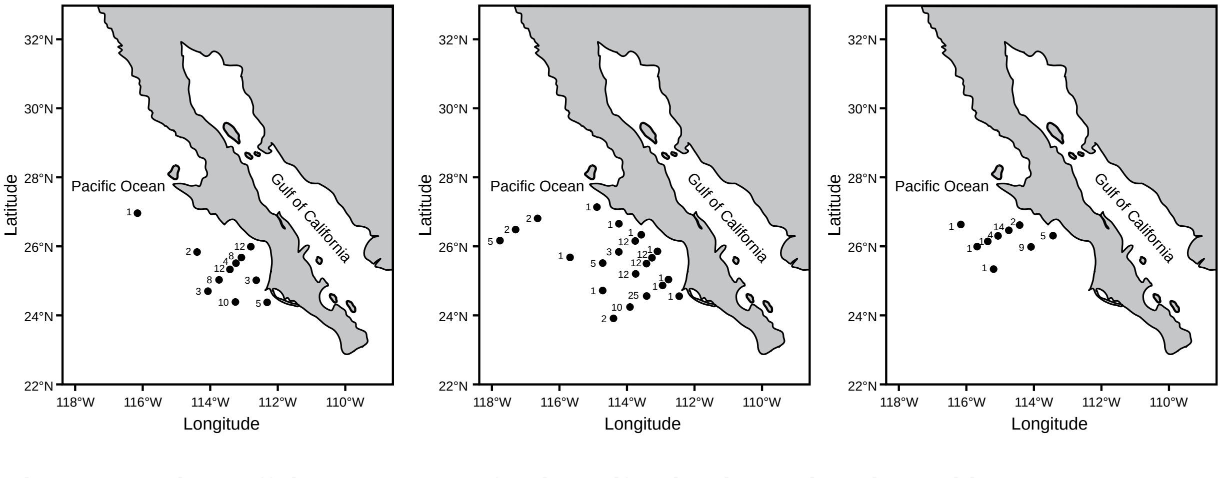


Figure 6. Stations off the west coast of Baja California where *Rhynchoteuthion* paralarvae were collected by the IMECOCAL programme.

Importance in the pelagic ecosystem of the Gulf of California

Caddy and Rodhouse (1998) proposed that recent increases in cephalopod biomasses can be explained by the reduction of predators. In the Gulf of California, there is evidence that the biomass of jumbo squid has increased in the last decade; but the effect of this increase on other groups of organisms, or the effect of changes in abundance of other groups on the jumbo squid, has not been analysed. For this reason, it is necessary to understand the ecological role of the jumbo squid in the pelagic ecosystem. In this study, we found that the energy transfer in the pelagic ecosystem of the central Gulf of California is top-down, and that the jumbo squid is a key species that maintains the balance of the populations at lower trophic levels, while the jumbo squid population is regulated from above by top predators and the fishery (Fig. 7; Rosas-Luis, 2005).

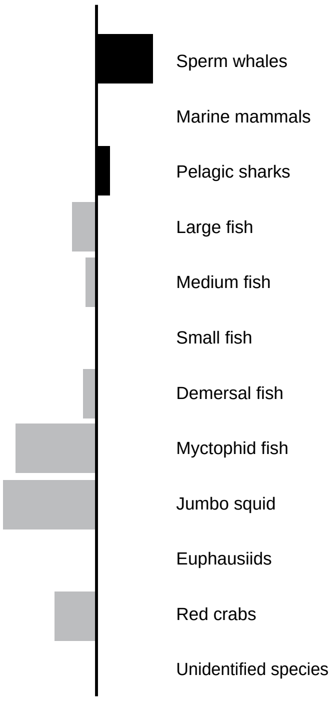


Figure 7. Positive effects (black bars) and negative effects (grey bars) imposed by jumbo squid on various components of the pelagic ecosystem, according to an ECOPATH model.

Age and growth

We compared growth parameters of jumbo squid among two areas, the Gulf of California and the west coast of Baja California (Table 1). The growth curves of the females were significantly different among areas, and the rate of growth (K) differed by two orders of magnitude. Nevertheless, the asymptotic length (Y_∞) differed of practically 2 cm. For the males, the growth curves were also statistically different, but the K's were similar and the Y_∞ were considerably different, with the Y_∞ of the males from the Gulf of California being larger (Mejía-Rebollo, 2006).

Table 1. Statistical comparison of growth parameters of jumbo squid sampled off the west coast (WC) of Baja California in 2004 and in the Gulf of California (GC) during 1995-1997 (Markaida, 2004), based on the integral logistic method. N=number of organisms, RSS=Residual Sum of Squares, MCR=Residual squares, * = highly significant, P<0.001**

Sex	N	Parameter	RSS	MCR	$F_{(3,385)}$	P
Female						
WC	143	Y_∞ = 877.5 K = 0.009536 T_o = 234.9	1255.39	8.9035	51.50	***
GC	247	Y_∞ = 896.1 K = 0.01065 T_o = 235.0	489250	2005		
Male						
WC	46	Y_∞ = 792.1 K = 0.01065 T_o = 214.3	328.4971	7.465	12.24	***
GC	133	Y_∞ = 842.1 K = 0.0116 T_o = 223.3	236077	1815		

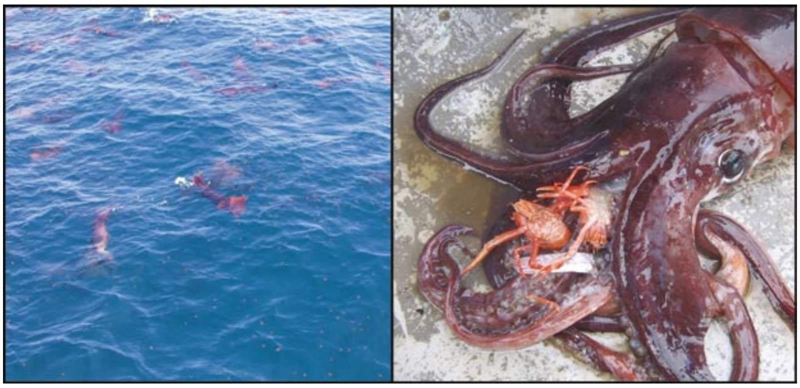


Figure 8. Jumbo squid feeding on red crabs at the surface during the day time.

Feeding

Preliminary results of feeding studies of jumbo squid conducted during 2004-2005 off the west coast off Baja California are summarised in Table 2. The main components of the diet and their percent composition by weight are shown.

During a research cruise on board the *BIP XII-CIBNOR*, jumbo squid were observed feeding on large numbers of red crabs (*Pleuroncodes planipes*) on the surface during the day (12:35 pm) at 23°26.84´N and 110°39.84´W (Fig. 8). Nine jumbo squid were collected; eight of them were females in maturity stages 3, 4 and 5 and one was a male in stage 5. The average MDL was 73.9 cm (♀) and 63.0 cm (♂).

Table 2. Percent composition by weight of organisms in the diet of jumbo squid collected off the west coast off Baja California

Prey	2004	2005
Pleuroncodes planipes	61.45	74.77
Vincingueria spp.	12.71	8.41
Myctophidae	2.78	2.04
Copepoda	10.25	
Pteropoda	2.72	0.51
Pisces	0.90	3.56
Octopoda	0.11	0.59
Teuthoidea	2.91	1.78
Unidentified organic material	1.63	2.21
Others	4.54	6.13

Climate: ENSO-jumbo squid relationships

During 1998, the squid fleet landed 7,466 t in San Carlos on the west coast of BC and 6,989 t in La Paz, BCS. This was due to the displacement of the jumbo squid outside the Gulf of California. In that year, the squid processors were located in Santa Rosalía, Mulegé, Loreto and Ciudad Constitution. Figure 9 shows that the landings in BCS were almost non-existent during this period, which followed a period with a negative Southern Oscillation Index during 1997-1999. In the winter of 2004-2005, this pattern occurred again, and part of the squid fleet moved towards Magdalena Bay, BCS. Movements by the jumbo squid during anomalous climatic events, like ENSO, must be considered by the processors in order to optimise their industrialisation and processing. A longer historical time series of landings is required to understand the relationships between jumbo squid and large-scale events such as the Pacific Decadal Oscillation and climate change.

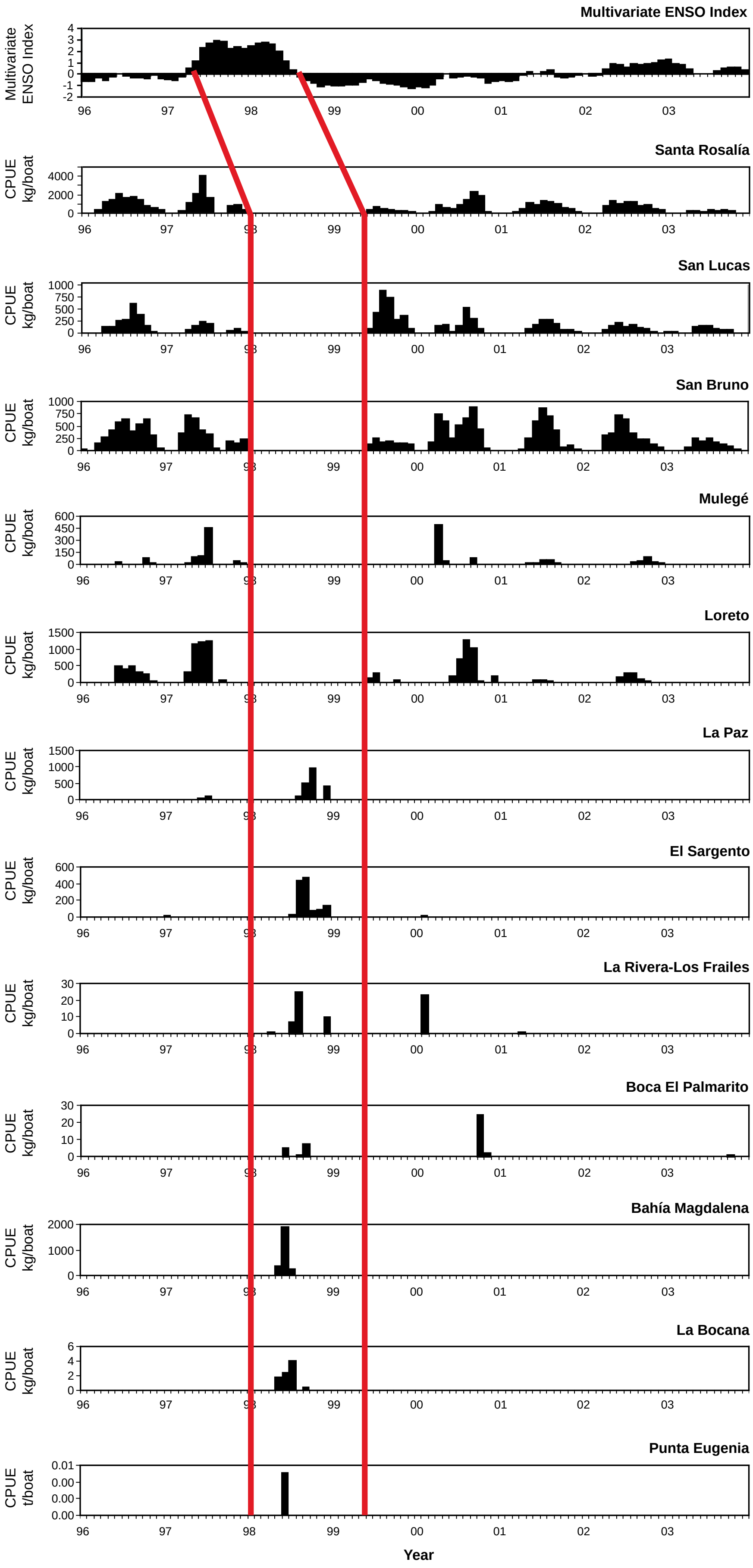


Figure 9. Relationship between the Southern Oscillation Index and jumbo squid landings during 1998 in Baja California Sur, Mexico.

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TROPHIC LINKS

Contribution of cephalopod prey to large pelagic fish diet in the central north Atlantic Ocean

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Open ocean ecosystems in the north Atlantic host a broad range of teleost predators, but underlying food web linkages supporting these large pelagic species remain poorly understood. In the 1950s and 1960s, exploratory longline sampling cruises were conducted by the R/Vs *Crawford* and *Delaware* of the US Bureau of Commercial Fisheries to identify potential tuna fishing grounds (see Wilson, 1965; Wilson and Bartlett, 1967). Diet components of large pelagic fishes were obtained from these offshore regions (Matthews *et al*., 1977). In the 1980s, Russian scientists also studied the ecology of offshore squid (Zuev *et al*., 2002), but much of this work remains untranslated.

Despite extensive longline fisheries in the central Atlantic, there is a surprising lack of ecological information available for this region. To better understand the trophic ecology of large pelagic species, stomach samples were collected from fish captured during directed longline research cruises in the central north Atlantic in 2001 and 2002 (Lutcavage and Luckhurst, 2001). The cruises were conducted primarily to target and sample bluefin tuna (*Thunnus thynnus*). Longline sets were made in offshore waters over a broad latitudinal range, extending from 43°N 54°W to 43°N 48°W (area 2) and 35°N 58°W to 37°N 52°W (area 1) from June to July 2001 and 23°N 71°W to 36°N 55°W (area 3) from May to June 2002 (Fig. 1). Additional sampling legs were conducted from June to October 2002 by the R/V *Shoyo Maru* (Satoh *et al*., 2004). A total of 83 stomachs were sampled in 2001 from Atlantic swordfish (*Xiphias gladius*) (n = 28), white marlin (*Tetrapturus albidus*; n = 2), blue marlin (*Makaira nigricans*; n = 1), albacore tuna (*Thunnus alalunga*; n = 24), bigeye tuna (*Thunnus obesus*; n = 14) and yellowfin tuna (*Thunnus albacares*; n = 14). A total of 107 stomachs were sampled in 2002 from Atlantic swordfish (n = 47), white marlin (n = 7), blue marlin (n = 2), longbill spearfish (*Tetrapturus pfluegeri*; n = 4), dolphinfish (*Coryphaena hippurus*; n = 11), albacore tuna (n = 12), bigeye tuna (n = 6) and yellowfin tuna (n = 18). No bluefin tuna were captured during either sampling year.

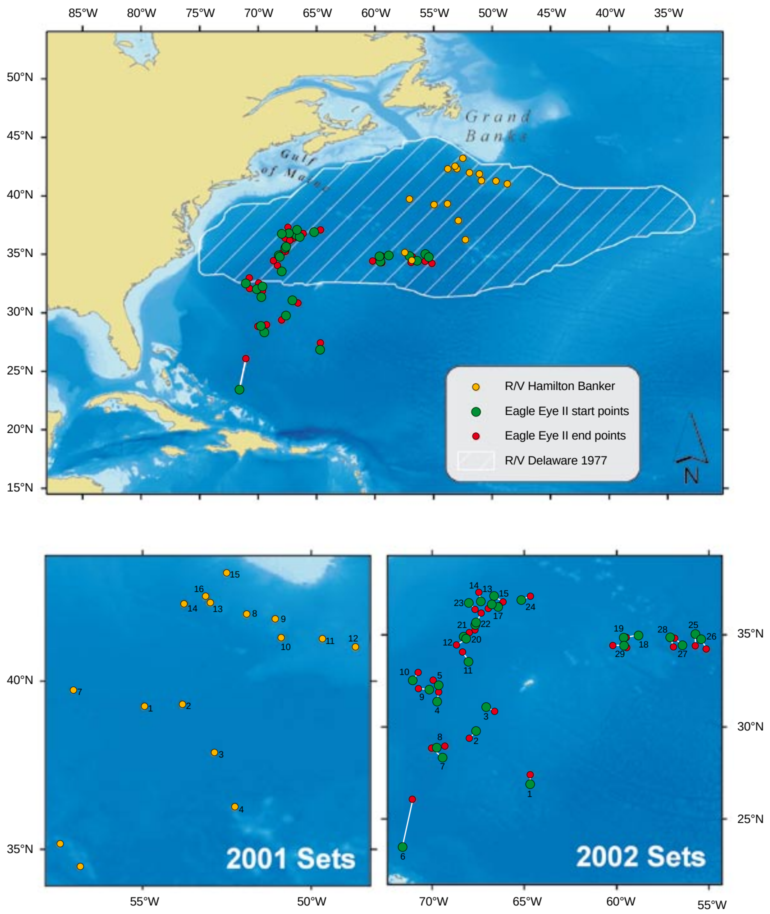

Figure 1. Longline set sampling locations for 2001 (areas 1 and 2) and 2002 (area 3).

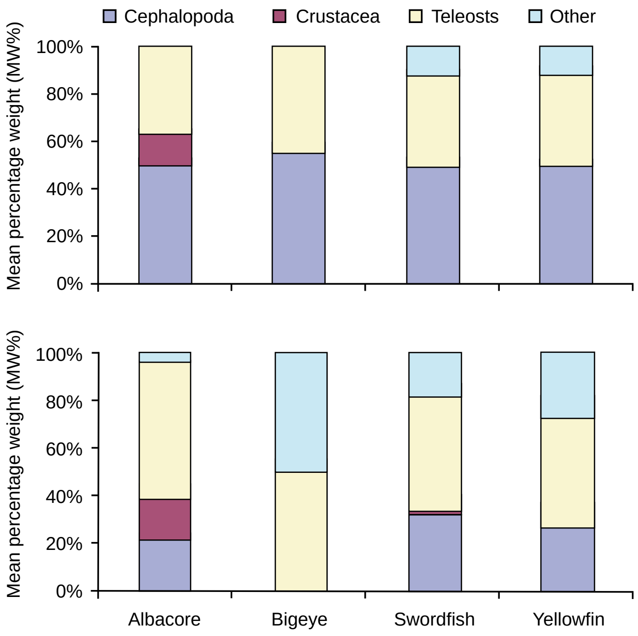

Figure 2. Mean percent weight of stomach contents from large pelagic fishes sampled in 2001 in a) area 1 and b) area 2.

Prey biomass of the large pelagic fishes sampled for 2001 and 2002 consisted mainly of cephalopods and teleost fishes (Figs. 2 and 3). The remaining stomach contents were composed mostly of crustacean prey, including decapod larvae and hyperiid amphipods, as well as trematode and nematode parasites. In 2001, cephalopods dominated the prey biomass for all species sampled in area 1, while teleost prey were more prevalent in area 2. In both areas, cephalopod prey consisted mainly of Ommastrephidae, with Gonatidae, Chiroteuthidae and Histioteuthidae also accounting for high proportions of cephalopod prey biomass in swordfish sampled from area 2. Teleost prey were dominated by families Paralepididae in area 1 and Bramidae and Myctophidae in area 2. Other major teleost prey included Triglidae, Alepisauridae, Stromateidae, Scorpaenidae, Carangidae, Balistidae, and Monacanthidae. In 2002, the cephalopod prey of all species sampled consisted almost entirely of Ommastrephidae. Cephalopods were dominant prey items of albacore and bigeye tuna, longbill spearfish, and Atlantic swordfish. Teleost prey consisted mainly of Alepisauridae and Scombridae for the billfishes, while tuna and dolphinfish consumed mostly Molidae and Exocoetidae, with fish comprising the largest prey biomass for white marlin, blue marlin, dolphinfish, and yellowfin tuna.

Along these broad ocean transects, the greatest overall prey biomass was comprised of Ommastrephidae, a widely distributed family of fast-swimming squid. Our stomach content results are similar to historical findings, demonstrating major contributions of Ommastrephidae to the diets of large pelagic fishes in the central north Atlantic (Matthews *et al*., 1977). Based on depth associations identified by studies using pop-up satellite archival tags (PSAT), Atlantic tunas and billfishes forage from the surface to at least 900 m, presumably in pursuit of cephalopod and teleost prey. Stomach samples from deeper-diving pelagic fishes, such as bigeye tuna and swordfish, contained the greatest diversity and proportional biomass of cephalopods. More surface-dwelling

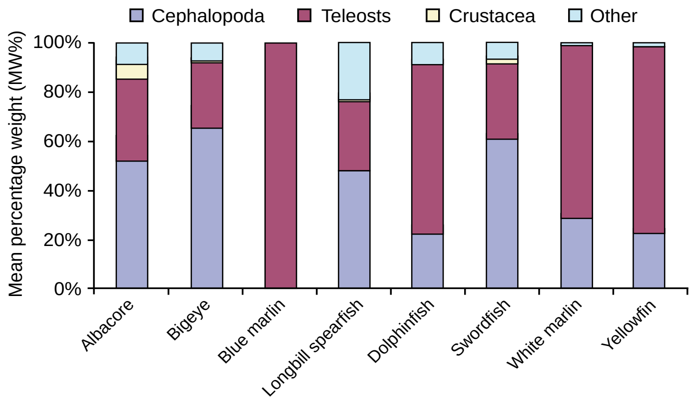

Figure 3. Mean percent weight of stomach contents from large pelagic fishes sampled in area 3 in 2002.

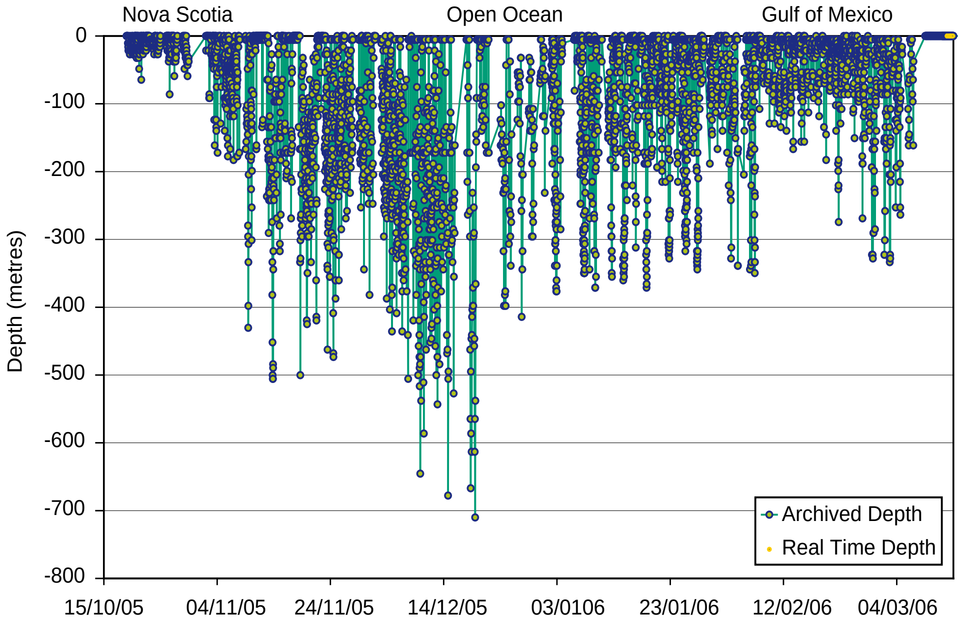

Figure 4. Depth distributions (m) of an Atlantic bluefin tuna (*Thunnus thynnus*) released with a PSAT off Nova Scotia, Canada in 2005.

pelagic fishes contained mostly Ommastrephidae. These preliminary stomach content analyses will be evaluated, along with stable isotope analyses of prey and predator tissues, in order to identify energy sources and trophic linkages in central north Atlantic food webs.

Although no bluefin tuna were sampled in the 2001-02 cruises, stomach content analyses conducted during the R/V *Delaware* cruises included mostly ommastrephid squid and teleosts of the families Bramidae and Balistidae (Matthews *et al*., 1977). A representative example of depth patterns of giant bluefin tuna tracked with PSATs in the central north Atlantic (Fig. 4) shows repetitive deep descents that suggest extensive foraging, presumably on bathypelagic cephalopods and fishes (M. Lutcavage, unpubl. data). Given the prominence of cephalopods in large pelagic fish diets, more studies are needed to identify their trophic relationships and distributions in oceanic regions.

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Cephalopod prey of the apex predator guild in the epipelagic eastern Pacific Ocean

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The stomach contents of apex predators provide valuable information about the biology of poorly-known prey species. The distribution and abundance of pelagic cephalopods is not well known, considering the difficulty of catching them with traditional methods. Sharks, tunas, billfishes, dolphins, and dolphinfishes are known to be important predators of cephalopods in the eastern Pacific Ocean (Perrin *et al*., 1973; Galván-Magaña *et al*., 1985, 1989; Abitia-Cardenas *et al*., 1997, 1998, 1999, 2002; Aguilar-Palomino *et al*., 1998; Markaida and Sosa-Nishizaki, 1998; Galván-Magaña, 1999; Olson and Galván-Magaña, 2002; Rosas-Alayola *et al*., 2002). A difficulty in studying cephalopods in the stomach contents of large predators is due to muscle tissue being digested quickly. Often, only the cephalopod mandibles (beaks) are found in stomachs after all the mantle tissue has been digested.

The predators sampled for stomach content analysis were caught by tuna purse-seine vessels fishing in the eastern Pacific Ocean (EPO) during two periods, 1992-1994 and 2003-2005 (Fig. 1). The study during 1992-1994 was sponsored by the US National Marine Fisheries Service, and was focused on investigating the relationship between yellowfin tuna and dolphins in the EPO. The study during 2003-2005 was sponsored by the Pelagic Fisheries Research Program, University of Hawaii, and the goal was to better understand food web dynamics in the pelagic eastern, central, and western equatorial Pacific based on stable isotopes and diet composition. The cephalopods were identified to the lowest taxon possible using morphological characteristics of the body and/or the mandibles. Whole cephalopods in an undigested state were identified from information in Okutani (1980), Roper *et al*. (1984) and Fischer *et al*. (1995), and cephalopod mandibles were identified based on Clarke (1962), Iverson and Pinkas (1971), Wolff (1982, 1984) and Clarke (1986). The cephalopod collections at the Santa Barbara Museum of Natural History and CICIMAR were used to validate the identifications. The frequency of occurrence and numbers of cephalopods found in the stomach contents were recorded by species.

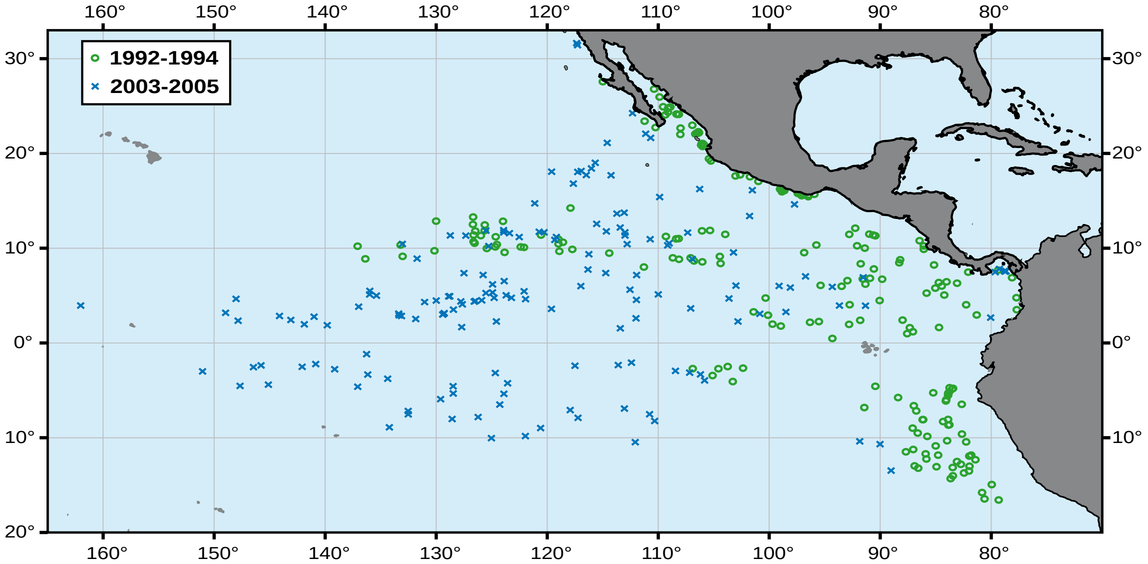

Figure 1. Map of set locations where predators were caught and analysed for cephalopod predation in two time periods.

Table 1. Predators caught in tuna purse seine sets in the eastern Pacific Ocean and sampled for stomach contents analysis during two sampling periods

Predator		**Number of samples**	
		1992-1994	**2003-2005**
Thunnus albacares	Yellowfin tuna	4831	937
Katsuwonus pelamis	Skipjack tuna	1205	310
Thunnus obesus	Bigeye tuna	80	82
Euthynnus lineatus	Black skipjack	100	37
Auxis spp.	Bullet tuna	55	20
Carcharhinus falciformis	Silky shark	326	290
Carcharhinus longimanus	Whitetip shark	30	4
Carcharhinus spp.	Other carcharhinids	84	
Sphyma spp.	Hammerhead shark	48	4
Isurus oxyrinchus	Mako shark	4	2
Prionace glauca	Blue shark	2	
Alopias spp.	Thresher shark	12	3
Nasolamia velox	Whitenose shark	2	
Makaira indica	Black marlin	25	
Makaira mazara	Blue marlin	15	14
Makaira spp.	Marlins	18	
Tetrapturus audax	Striped marlin	8	1
Istiophorus platypterus	Sailfish	49	1
Coryphaena spp.	Mahi-mahi	545	295
Acanthocybium solandri	Wahoo	235	417
Stenella attenuata	Spotted dolphin	311	
Stenella longirostris	Spinner dolphin	209	
Delphinus delphis	Common dolphin	51	
Stenella coeruleoalba	Striped dolphin	5	
Total		**8250**	**2417**

A total of 10,667 stomach samples taken from a suite of predators during both sampling periods were analysed for this study (Table 1). Twenty-five cephalopod genera or species were identified, based mostly on the beaks. The octopods recorded were: *Argonauta nouryi*, *Argonauta pacifica*, *Argonauta cornutus*, *Argonauta* spp., *Japetella diaphana*, *Octopus rubescens*, *Tremoctopus violaceus*, *Alloposus mollis*, *Vitreledonella richardi*, and *Vampyroteuthis infernalis*. The decapods were: *Ancistrocheirus lessueuri*, *Octopoteuthis deletron*, *Thysanoteuthis rhombus*, *Dosidicus gigas*, *Sthenoteuthis oualaniensis*, *Onychoteuthis banksii*, *Pholidoteuthis boschmani*, *Abraliopsis falco*, *Abraliopsis affinis*, *Mastigoteuthis dentata*, *Mastigoteuthis* spp., *Loligo opalescens*, *Loliolopsis diomedeae*, *Liocranchia reinhardtii* and unidentified loliginids.

We compared the cephalopods consumed by the predators grouped in taxonomic categories: sharks, tunas, billfishes, dolphinfishes, wahoo and dolphins. Our comparisons were based on the frequency of occurrence and number of prey consumed during each sampling period. Cephalopod remains were found in the stomach contents of the tunas, wahoo (*Acanthocybium solandri*) and rainbow runner (*Elagatis bipinnulata*) more frequently in the 2003-2005 period than in the 1992-1994 period, while sharks, billfishes and dolphinfishes consumed cephalopods more frequently in the earlier period than in the later period. The Humboldt squid (*Dosidicus gigas*), however, was consumed by the tunas, wahoo, rainbow runner, sharks, billfishes and dolphinfishes more frequently during the 1992-1994 period. *D. gigas* comprised the greatest proportion, by number, of the total cephalopod predation by the tunas and billfishes in the 1992-1994 period, and by the dolphinfishes, billfishes,

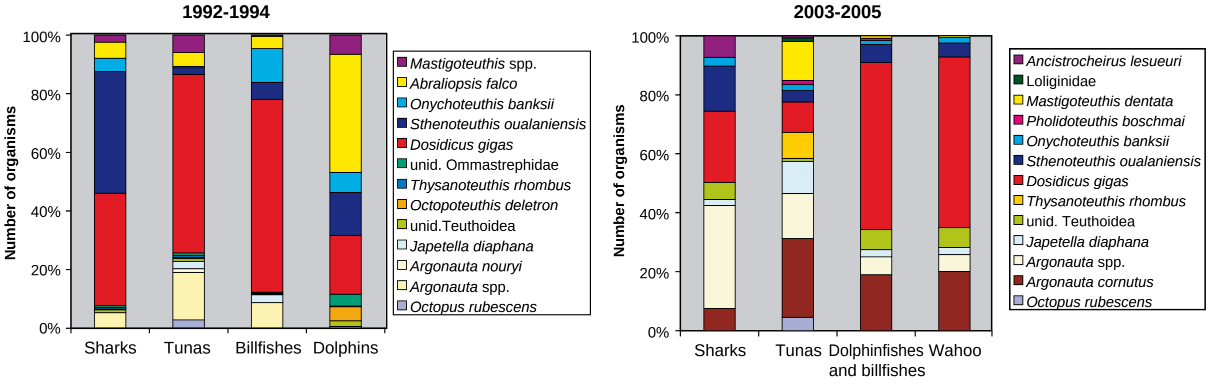

Figure 2. Taxonomic composition of the total cephalopod predation, in percent number of organisms, by several predator groups in the 1992-1994 and 2003-2005 studies.

and wahoo in the 2003-2005 period (Fig. 2). The sharks ate greater proportions of *Sthenoteuthis oualaniensis* in the earlier period and *Argonauta* spp. in the later period. The dolphins ate more *Abraliopsis falco* than any other cephalopod taxon during 1992-1994 (Fig. 2). We also examined predation on epipelagic versus mesopelagic cephalopods by the various predator groups. *Dosidicus gigas*, *S. oualaniensis*, *Onychoteuthis banksii* and argonautids were the main epipelagic cephalopods and *Japetella diaphana* and *Mastigoteuthis* spp. were the main mesopelagic cephalopods consumed by the upper-trophic predators in the EPO. We will expand on this analysis in the near future, by examining the spatial and size-specific characteristics of cephalopod predation.

We consider that large predators are relatively unbiased samplers of the cephalopod fauna compared with nets used to sample nekton. Although cephalopod mandibles often accumulate in the stomach contents, the high frequency of occurrence and number of cephalopods consumed by large predators in the EPO indicate that pelagic squid and octopods are important components of the food web. Pelagic cephalopods are also important prey of birds and marine mammals, and in turn, are important predators of crustaceans and fishes at lower trophic levels (Markaida and Sosa-Nishizaki, 2003). The differences in cephalopod predation by the various predators suggest differences in foraging behaviour and habitat use.

The vertical habitat of cephalopods has important implications on their rates of predation. Some cephalopods, such as *Argonauta cornuta*, *A. noury*, *A. pacificus*, *Ancistrocheirus lesueuri*, *Loligo opalescens* and *Loliolopsis diomedeae* occur close to the surface (0-125 m). Cephalopods are known to undertake vertical migrations at night (Clarke and Lu, 1975; Roper and Young, 1975) and this behaviour makes them vulnerable to epipelagic predators when they are closer to the surface. The species that vertically migrate from deep waters (1500 m) to the surface include *D. gigas*, *S. oualaniensis*, *Pholidoteuthis boschmai*, *T. rhombus*, *O. banksii* and *Alloposis mollis*. Other cephalopods vertically migrate from deep waters to mesopelagic waters (2000 - 200 m) and these include *A. affinis*, *A. falco*, *Mastigoteuthis* spp., *V. infernalis*, *Japetella heathi*, and *V. richardi*. Some predators (mainly sharks) are known to forage on cephalopods in deep waters.

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New information from predator diets on the importance of two Ommastrephidae: *Sthenoteuthis oualaniensis* in the Indian Ocean and *Hyaloteuthis pelagica* in the Atlantic Ocean

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Squid are widely distributed in the open ocean, where they constitute a key group in marine food webs (Rodhouse and White, 1995). They are among the most abundant in number and biomass of nektonic epipelagic organisms, and the large squid of the family Ommastrephidae (e.g. *Dosidicus* and *Illex*) support major fisheries in both neritic and oceanic waters around the world (Rodhouse, 1997). This commercial importance has made the large ommastrephids the target of many scientific investigations, and consequently their biology is reasonably well-known (Nigmatullin *et al*., 2001; Zuyev *et al*., 2002; Bower and Ichii, 2005; Markaida, 2006). However, the biology and ecological role of the unexploited squid species remain poorly known in many areas of the world ocean. Research cruises devoted to the study of squid are few, and in addition, cephalopods are difficult to collect by nets. Large pelagic fishes (e.g. tunas and tuna-like species), mammals and seabirds can be efficient biological samplers for collecting information on cephalopods, due to their opportunistic feeding behaviour (Cherel and Weimerskirch, 1999; Potier *et al*., 2007). In addition, cephalopod predators catch larger specimens and a greater diversity of species than sampling gear (Rodhouse, 1990; Cherel *et al*., 2004). In the stomach contents of large pelagic predators, cephalopod beaks, indigestible hard structures, accumulate over time. The beak morphology allows identification to species level of most of the accumulated items found in predators' stomachs (Clarke, 1986; Imber, 1992). Therefore, the description of dietary habits, which allows a better understanding of trophic interactions in the marine ecosystems, can also provide useful information on species composition, distribution, abundance and ecology of cephalopods occurring within the predators' foraging range. In this note, we illustrate the usefulness of cephalopod predators for describing the importance of *Sthenoteuthis oualaniensis* (Ommastrephidae) in the pelagic food webs of the western Indian Ocean, and of *Hyaloteuthis pelagica* (Ommastrephidae) in the Atlantic Ocean.

In the Indian Ocean, the biomass of the purpleback squid *S. oualaniensis* has been estimated to be approximately 2 millions tonnes (Zuyev *et al*., 1985). In the northern part of the Arabian Sea, its density could reach up to 4-8 tonnes km^{-2} (Gutsal, 1989), although the population structure of *S. oualaniensis* is poorly known. Nesis (1993) described three different forms, which differ by anatomy, geographic distribution and period of spawning: (1) the giant form is found exclusively in the Red and Arabian Seas; (2) the dwarf form, with no photophores, inhabits the equatorial waters of the Indian Ocean, and spends most of its life in the upper mixed layers; (3) the third form, characterised by photophores on the mantle, is the most common, and has a wider geographic repartition with a much deeper vertical distribution than the dwarf form.

In the equatorial waters surrounding the Seychelle Islands, *S. oualaniensis* constituted a dominant or a significant prey in the diet of swordfish and subsurface tunas (yellowfin and bigeye) caught by a longliner (Potier *et al*., 2007). *S. oualaniensis* accounted for 19.1% and 15.9% of the whole reconstituted weight, and contributed 13.3% and 9.0% by number in the diet of yellowfin tuna and swordfish, respectively (Potier *et al*., 2007). In Russian studies that have been carried out in the same area, *S. oualaniensis* represented 26.7% and 15.1% of the total index of relative importance (IRI) in the diet of subsurface yellowfin and bigeye tunas (no published data). However, stomach content analyses of tunas caught by surface purse-seine fisheries in the same area have shown that *S. oualaniensis* did not contribute significantly to the diets: it represented only 3.2% and 0.1% by number in the diet of yellowfin and bigeye tunas (Potier *et al*., 2004). Such tunas caught by purse seiners occur generally in dense schools at the surface and several studies have shown that these tunas seek out and feed on large concentrations of monospecific prey (Bard *et al*., 2002; Ménard and Marchal, 2003; Potier *et al*., 2004). Once a concentration is detected, feeding involves successive capture of individuals of the same species. Therefore, in the equatorial waters surrounding the Seychelles, we hypothesize that the purpleback squid does not occur in concentrations that are sought out by surface predators during the daylight hours. However, purpleback squid can also undertake diel migration in order to avoid predators chasing at the surface during daytime.

The size distribution of the beaks of the purpleback squid found in the stomachs of yellowfin tuna and swordfish are clearly different (Fig. 1): swordfish catch larger specimens than yellowfin tuna. Swordfish are known to undertake large vertical migrations, enabling them to prey actively at greater depths than yellowfin tuna. Therefore, it can be assumed that *S. oualaniensis* adults, which are fed on by swordfish, have a greater vertical range than the juveniles, which are fed on by yellowfin tuna. On the other hand, it is possible that the two predators could feed on two forms of *S. oualaniensis,* each having different size and bathymetric distributions (Nesis, 1993).

Russian studies have shown that the importance of the purpleback squid in the diet of large fish predators decreases in the tropical waters around Mauritius (6.2% of the IRI for subsurface yellowfin tuna; unpublished data). Furthermore, preliminary studies conducted in the Mozambique Channel have shown that another ommastrephid (*Ommastrephes bartrami*) has replaced *S. oualaniensis* in the diet of swordfish. However, *S. oualaniensis* plays a major role in the diet of tropical seabirds breeding on islands in the Mozambique Channel. This prey species contributed 19% by number in the diet of great frigatebirds (Weimerskirch *et al*., 2004) and 15.4% by reconstituted weight in the diet of the red-tailed tropicbird *Phaeton rubricauda* (Le Corre *et al*., 2003). In the diet of the sooty tern *Sterna fuscata*, *S. oualaniensis* occurred in 53% of the stomachs sampled on Europa and Glorieuses Islands and was ranked first by the IRI. On Juan de Nova Island, *S. oualaniensis* occurred in 33% of the stomachs and ranked third by the IRI (Jaquemet *et al*., in prep). Figure 1 displays the size distribution of the beaks found in the stomachs of sooty terns. Sooty terns catch the smallest specimens of *S. oualaniensis* (with mean sizes significantly different for the three predators). We suspect that the three forms of *S. oualaniensis* that were described by Nesis (1993) are found in the Mozambique Channel..

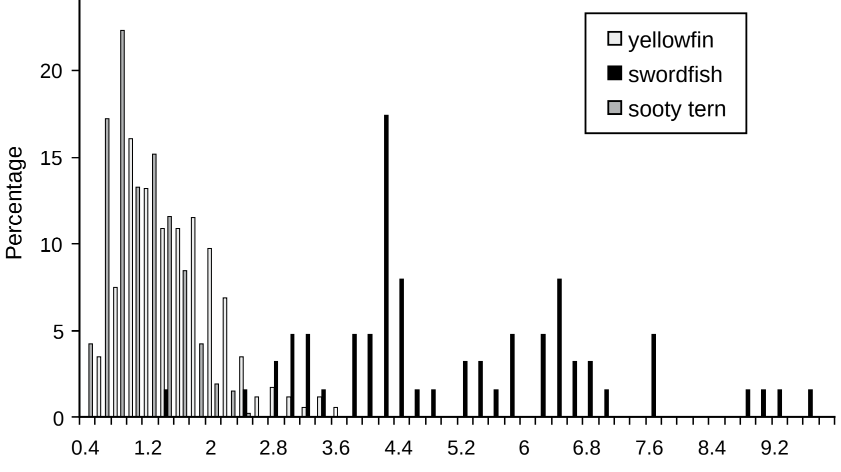

Figure 1. Frequency distribution of lower rostral lengths (LRL) (mm) of the beaks of *Sthenoteuthis oualaniensis* eaten by yellowfin tuna, sooty tern and swordfish in the western Indian Ocean.

In a recent study, Cherel *et al*. (2007) described the importance of the glassy flying squid *Hyaloteuthis pelagica,* Bosc, 1802 in the diets of large pelagic fishes sampled in the central tropical Atlantic Ocean. *H. pelagica* is the smallest ommastrephid, reaching a maximum mantle length of only 90 mm (Nesis, 1987). *H. pelagica* was by far the most important cephalopod prey of the community of large predatory fishes sampled during research cruises in autumn 2000. *H. pelagica* was a major prey of white marlin (*Tetrapturus albidus*) and a common food item of albacore (*Thunnus alalunga*), longbill spearfish (*T. pfluegeri*) and sailfish (*Istiophorus albicans*). All fishes fed upon the same size range of *H. pelagica*, including both juvenile and adult squid, but overall the fishes preyed on squid of different mean sizes: white marlin and longbill spearfish fed more on adult squid than did albacore and sailfish. The ommastrephid *Sthenoteuthis pteropus*, usually abundant in the tropical Atlantic Ocean, was surprisingly absent in fish diets in the study of Cherel *et al*. (2007). The authors hypothesize that *S. pteropus* was not an important and available nektonic prey organism at the time of sampling.

These two examples emphasise the usefulness of marine predators to gain valuable information on the biology and the distribution of their prey. In addition, our studies show that cephalopods constitute a link in the transfer of energy from lower trophic levels (most likely mesozooplankton) to higher trophic levels (including tunas, billfishes and swordfish).

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Trophic ecology of jumbo squid *Dosidicus gigas* in the Gulf of California and adjacent waters

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Jumbo squid *Dosidicus gigas* currently leads world cephalopod catches and is perhaps the most abundant middle-sized predator in the eastern Pacific Ocean. Since 1995, we have analysed the stomach contents of 1,259 jumbo squid from the Gulf of California and adjacent waters in order to discern its trophic role and feeding habits. Hard remains (fish otoliths, squid beaks) were mainly used to identify the prey. Prey %N, %FO and %W were used to quantify the diet.

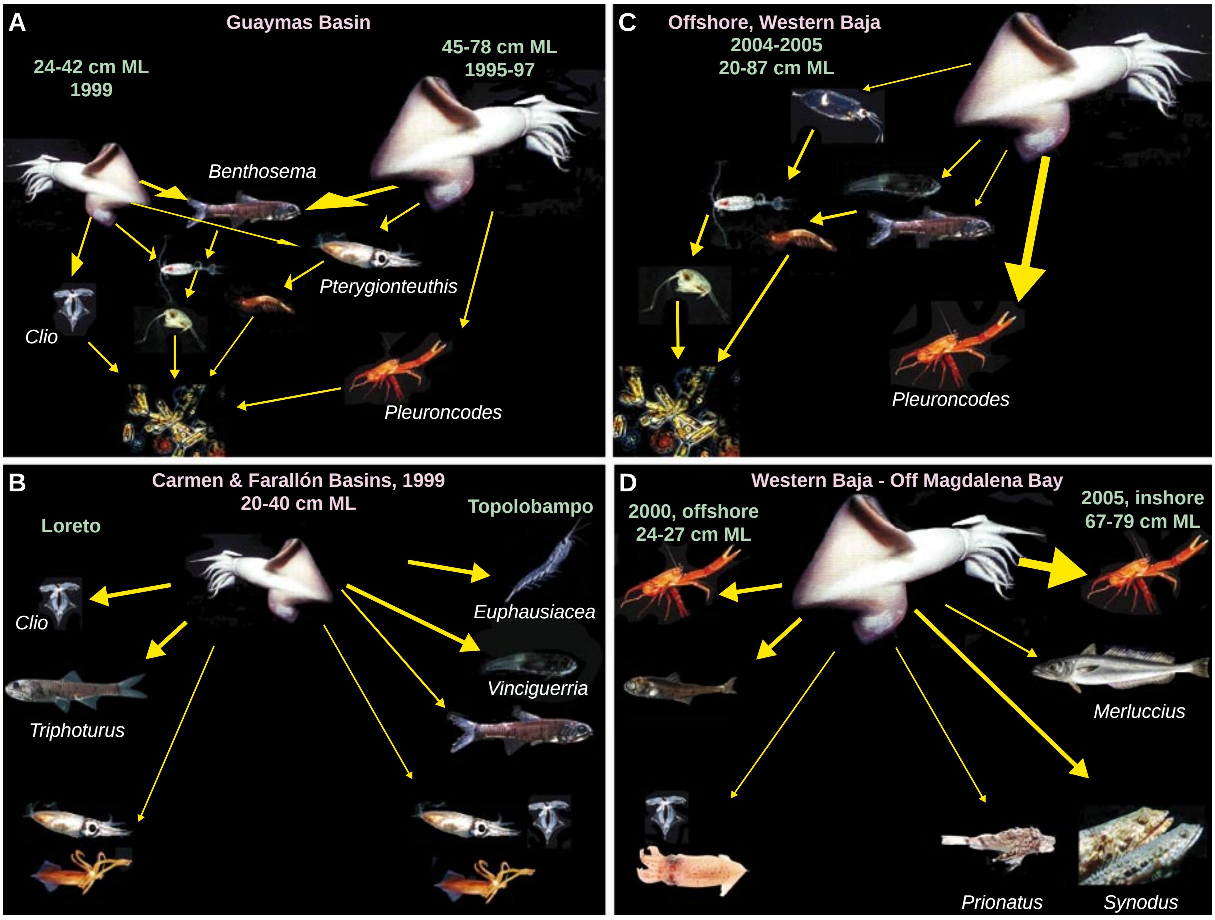

Figure 1. Trophic relations of jumbo squid from the Guaymas Basin in the Gulf of California for A) two different maturing sizes, B) southern basins of Carmen and Farallon, C) squid from western Baja California peninsula in offshore waters and D) off Magdalena Bay in offshore and inshore waters.

The Guaymas Basin, in the Gulf of California, may be considered the primary habitat for this squid, where they are abundant all year round, supporting >95% of the catches. Large jumbo squid in the basin feed on mesopelagic micronekton, mainly the nyctoepipelagic myctophid *Benthosema panamense*, and to lesser degree on another lanternfish, *Triphoturus mexicanus*, micronektonic squid and crustaceans (Markaida and Sosa-Nishizaki, 2003). This pattern was also observed during post-*El Niño* conditions, when medium-sized squid were found in the Gulf (Markaida, 2006; Fig. 1a). In southern basins of the Gulf, other mesopelagic fishes such as *T. mexicanus* and *Vinciguerria lucetia* dominate the diet instead of *Benthosema* (Fig. 1b). Thus, *Dosidicus* depends on a little known but important food chain based on annual prey, whose productivity is far larger than their standing stock. Squid diel vertical migrations revealed by our research (Gilly *et al*., 2006) are consistent with the feeding on this micronektonic assemblage, which is associated with deep scattering and oxygen minimum layers. Research on these prey and their habitat is critical to properly understand large fluctuations in squid abundance and changes in their population structure.

Off western Baja California, the jumbo squid diet is largely dominated by the pelagic red crab *Pleuroncodes planipes*. This galatheid is the main grazer and an important prey for most pelagic predators in the area. Thus, *Pleuroncodes* shortens the pelagic food chain by one step, contributing to a more efficient energy transference (Kashkina and Kashkin, 1994). Secondary prey off western Baja include a much larger diversity of micronektonic myctophids than inside the Gulf, where there is a less-developed oxygen minimum layer (Fig. 1c).

Dosidicus caught in inshore waters of western Baja, although still dependant on *Pleuroncodes*, also feed on neritic fishes, including lizardfish and hake (Fig. 1d). This is important to note in the view of recent expansions of the range of this abundant squid. Jumbo squid invasions on the continental shelf may impact on other food chains and on valuable commercial fishes. However, it is unlikely that this kind of prey, whose annual production is smaller than their standing stock, may support large squid abundances for long periods of time.

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The jumbo squid, *Dosidicus gigas*, a new groundfish predator in the California Current?

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The jumbo squid (*Dosidicus gigas*) is an important component of subtropical food webs, as both a major predator of forage fishes and an important prey item for tunas, billfishes and marine mammals. While the usual range of jumbo squid extends through the coastal and pelagic waters of the eastern tropical Pacific Ocean, and north into the Gulf of California, they have been sporadic visitors in the waters off California over the last century. They were particularly abundant off of central California for several years during the mid 1930s, when they were described as a nuisance to both commercial and recreational fishermen (Croker, 1937). Beginning in the late 1990s, and especially from 2004-2006, jumbo squid were observed in substantial numbers off California and as far north as Alaska. Significant occurrences of these squid have appeared in research surveys along the west coast of the US, in commercial fishing operations, and in the stomachs of California sea lions from the southern California bight. California Commercial Passenger Fishing Vessels have begun targeting these squid for recreational customers since the late 1990s, with particularly high landings off central California during the winter months (January through March) in 2005 and 2006. Animals collected from California waters seem to show growth patterns comparable to animals off of Baja California, with smaller animals in May and June, progressively larger animals during the summer and early autumn, and the largest animals during the winter months.

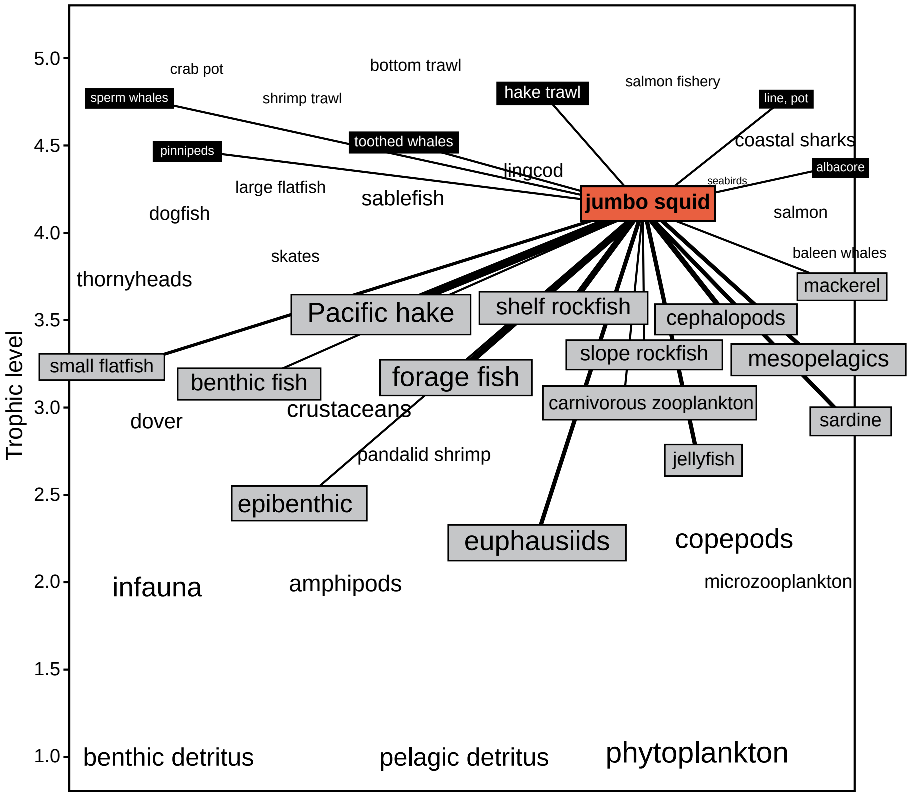

Figure 1. Food web model of the California Current, with a focus on jumbo squid and their known or suspected predators,including fisheries, (in black) and prey items identified in this study (grey). The estimated trophic level is along the y axis, the height of the boxes is scaled to the log of the standing biomass, and the width of the bars represents biomass flux of prey to predators.

To evaluate their potential impacts on the food web, particularly on commercially important groundfish, we opportunistically collected over 400 stomach samples between 2005 and 2006 at various sites along the California coastline. Stomachs were initially frozen or stored in ethanol, and when processed, contents were weighed and identified to the lowest taxonomic level possible. As with most cephalopod food-habit studies, prey identifications were made from otoliths, beaks, scales, bones and other hard parts, based on both published guides and reference collections. Additionally, standard lengths (for fishes) and mantle lengths (for cephalopods) were reconstructed based on published and fitted regressions against otolith lengths and rostrum lengths, where possible. Estimates of prey weight were then reconstructed from weight-length relationships for those items that were identifiable to species level. Results confirm that *Dosidicus* are indeed capable of predation on adult groundfish, as well as being significant predators on a wide range of forage species, as the ten most frequently encountered species or taxonomic groups (in descending order of importance) were Pacific hake (*Merluccius productus*), northern lampfish (*Stenobrachius leucopsarus*), northern anchovy (*Stenobrachius leucopsarus*), other jumbo squid, Pacific sardine (*Sardinops sagax*), blue lanternfish (*Tarletonbeania crenularis*), shortbelly rockfish (*Sebastes jordani*), unidentified rockfish (*Sebastes* spp.), *Euphausiidae*, and California headlightfish (*Diaphus theta*). When the average weight of prey items was taken into account, the importance of groundfish as prey items increased relative to that of mesopelagic fishes. Approximately 40 additional species or taxonomic groups were also observed.

We also used the resulting food habits information in an altered version of an existing ecosystem model of the Northern California Current (Field *et al*., 2006), to include jumbo squid solely for the purpose of graphically representing their relative trophic role in the California Current food web. Production and consumption rates were taken from Olson and Watters (2003), which in turn were based on Ehrhardt (1991). Together with the food habits data, the model indicates that *Dosidicus* are significant higher-trophic-level predators in the California Current ecosystem, with much of their diet comprised of commercially important groundfish and coastal pelagic species (Fig. 1). By contrast, they tend to be prey for many commercially important species in semi-tropical and tropical waters of the Pacific (Olson and Watters, 2003). This is consistent with the widely held notion that jumbo squid are opportunistic predators, capable of feeding on a wide range of prey items throughout the eastern Pacific Ocean. Although the impact on the ecosystem is hard to infer, given the lack of abundance data, the potential impact could be substantial, particularly due to the mismatch of tropical versus temperate life histories.

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Artisanal catches of jumbo squid, *Dosidicus gigas,* off Coquimbo, Chile and their relation to environmental variables

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Introduction

The jumbo squid, *Dosidicus gigas*, is an important cephalopod in the eastern Pacific Ocean. According to Rocha and Vega (2003), *D. gigas* had been fished sporadically by small-scale and industrial fishing fleets in Chile since 1957. Schmiede and Acuña (1992) recorded a large increase in catches in 1992, and suggested that *D. gigas* could be an interesting potential new resource for the artisinal fleet in the zone of Coquimbo. Fernández and Vásquez (1995) analysed the 1991-1994 fishing period, and characterised it as an ephemeral mainly industrial fishery, based primarily on the fact that more than 80% of the landings in 1994 were from factory vessels. The characteristics of the current fishery for *D. gigas*, during its latest appearance in the zone of Coquimbo, are drastically different from the previous period. Acuña *et al*. (submitted) analysed the evolution of this fishery from 2001 to 2005, and described the fleet, catches, effort, CPUE and some biological parameters during that period.

This paper describes some biological parameters of *D. gigas* and the latest development of the artisanal fishery in the area of Coquimbo during late 2005 and 2006, as well as relationships between the catches and some environmental variables during 2001-2006.

Methods

The study area was the zone of Coquimbo, between latitudes 29°12'S and 31°00'S. Data on jumbo squid catches were obtained from the official fishery statistics of the Chilean National Fisheries Service (SERNAPESCA) and from records of the artisanal fishermen. Data on mantle length (ML, 1 cm precision), weight (1 kg precision) and sex were recorded during 2006.

The relative abundance was analysed using the catch per unit of effort (CPUE), with effort defined as a fishing trip with catch, following Leos (1998). To determine if there were causal relationships between the CPUE and environmental factors, the methodology of Pierce and Haugh (1977) was followed, and corrected by the method of Box *et al*. (1994).

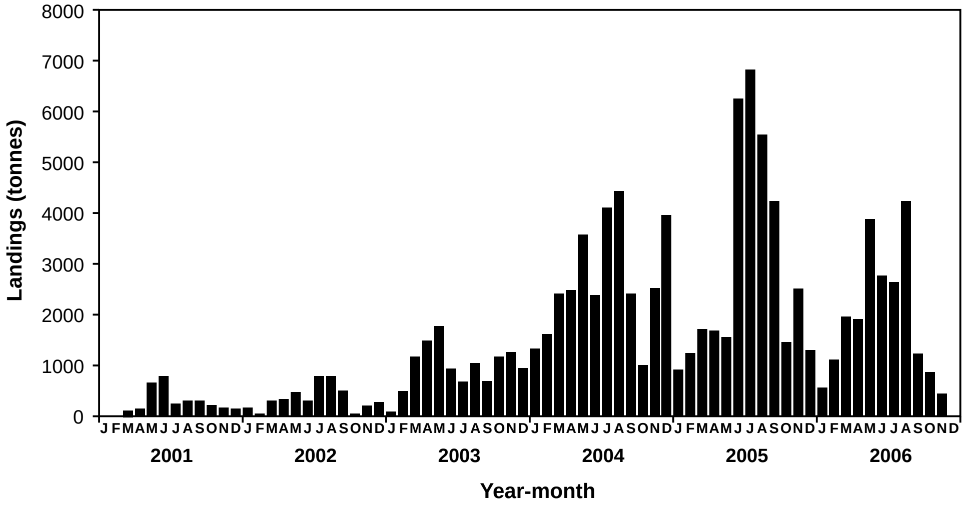

Figure 1. Catches/landings of *D. gigas* in the zone of Coquimbo, 2001-2006, by month and year.

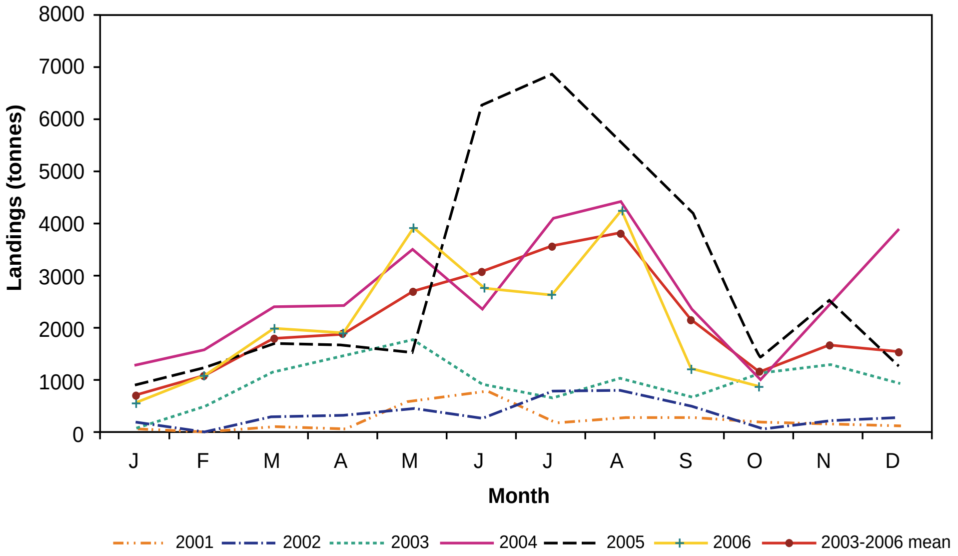

Figure 2. Monthly catches/landings of *D. gigas* in the zone of Coquimbo during the 2001-2006 period.

Results

1) Catches/landings. The jumbo squid catches/landings in the IVth Region increased during the study period, with the greatest catches/landings during 2005 (Fig. 1). These catches/landings were taken mainly during the first semester, with a maximum in August, decreasing in September and October, and recovering in November (Fig. 2). This decrease seems to be due to the squid migrating offshore for reproduction, at least out of the range of the boats. This feature is more apparent during the 2003-2006 period, when a processing plant was fully operative. During 2006, the catches decreased relative to the previous year, although they were significantly greater than those of 2001 to 2003 (Fig. 2).

Of the *D. gigas* catches in the IVth Region during 2001 to 2006, 99.7% were taken by artisanal boats for which *D. gigas* was the target species, and 98.6% were taken in the zone of Coquimbo. The boats were from the ports of Coquimbo, Guayacán, Guanaqueros and Tongoy.

2) CPUE. The monthly CPUE time series showed an increasing tendency during the study period to a maximum in May-July 2006 (Fig. 3). The CPUE values typically declined toward the end of each year, suggesting a drastic decrease in availability, especially during 2004 and 2005 (Fig. 3).

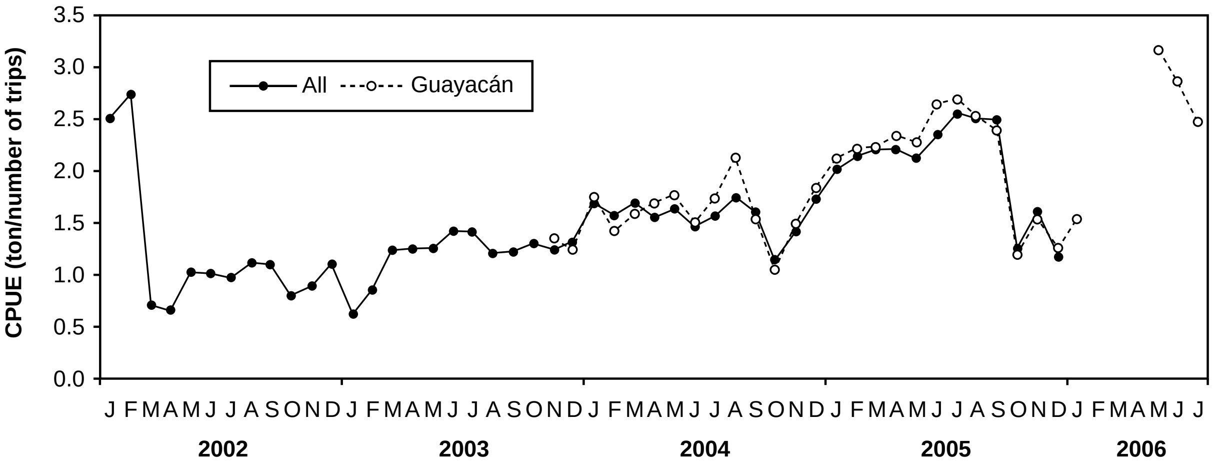

Figure 3. Monthly time series of catch per unit of effort (CPUE) for the port of Guayacán and for all ports, 2001-2006.

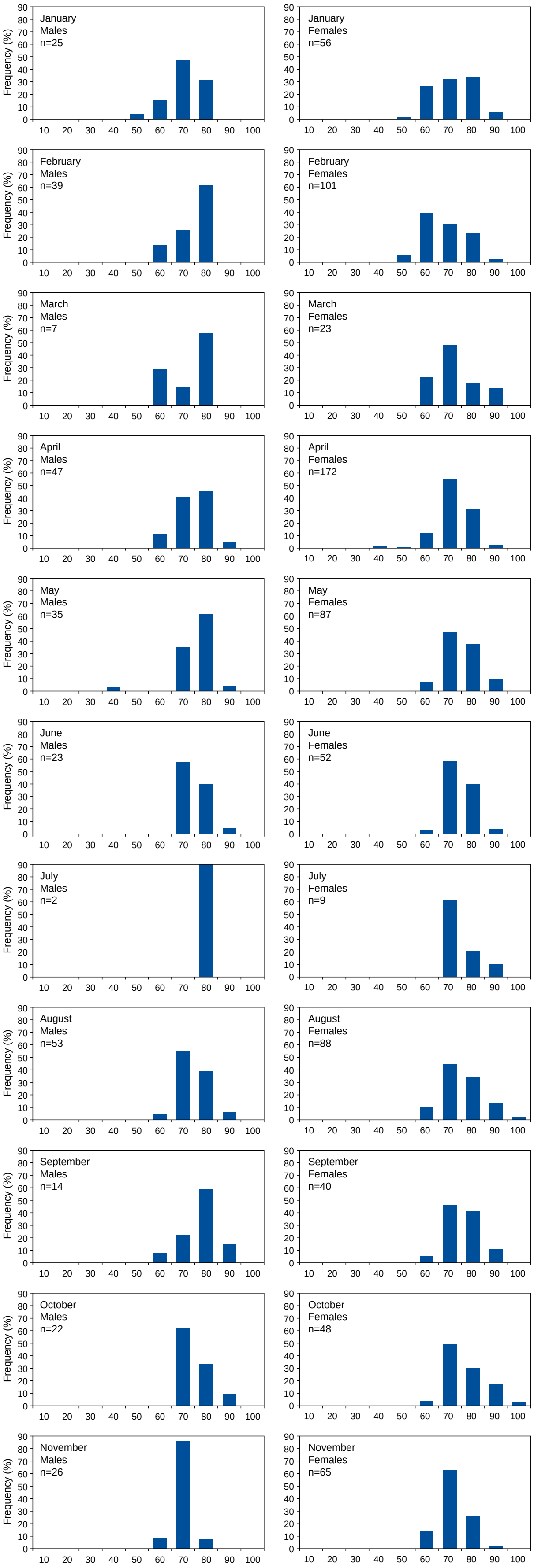

Figure 4. Mantle length percent-frequency distributions in male and female jumbo squid collected during 2006.

3) Biological aspects. Length-frequency distributions (mantle length, ML) for jumbo squid collected during 2006 showed a size range from 40 to 102 cm, with modes between 63-67 cm in males and 68-72 cm in females (Fig. 4).

4) Relationship with environmental variables. The apparent relationship between jumbo squid catches and different environmental variables, especially related to *El Niño - La Niña*, was explored. Two environmental time series were considered as input variables, the sea-surface temperature of the *Niño*1+2 area (N1+2) and the Southern Oscillation Index (SOI; NOAA, Climate Prediction Center), for the period February 2001 to November 2006. An autoregressive-moving average (ARMA) (1, 2, 4; 1) was fitted to the SOI series, and an ARMA (2; 2) to the N1+2 series. The seasonal/annual component was removed from all series, and a linear trend was removed from the catch/landing series prior to the fitting process.

The results of the analysis for the SOI indicated a significant cross-correlation at 6 months lag, (P = 0.033) (Fig. 5). For the N1+2 input variable, a significant cross-correlation at 5 months lag (P = 0.037) was found (Fig. 6).

Discussion

The fishery for jumbo squid in the zone of Coquimbo during 2001-2006 was primarily an artisanal fishery, in contrast to the 1991-1994 period when an industrial fleet was responsible for most of the landings (Fernández and Vásquez, 1995).

Taipe *et al*. (2001) indicated that jumbo squid are most abundant in the oceanic area off Perú (over 20 nm) in the autumn, winter and spring, and disperses out during the summer. This pattern was also very clear in the catch and CPUE time series in the squid fishery off Coquimbo, although the decrease is found in the spring during October. This decrease in availability during the spring in the coastal zone is probably due mainly to the fact that the small artisanal boats can not follow the squid as they migrate offshore (outside 12 nm from the coast). This offshore migration seems to be related to the reproductive cycle of *D. gigas* in the area of Coquimbo, because large specimens can be caught again one month later (November) within 12 nm of the coast.

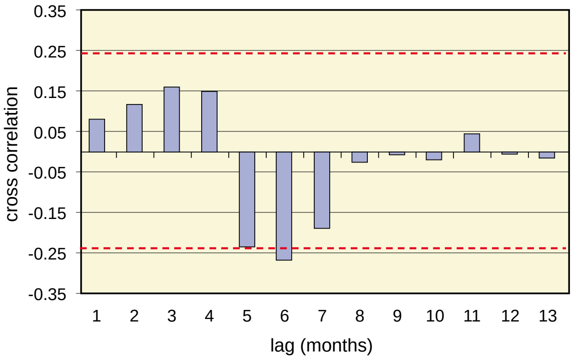

Figure 5. Cross-correlation function for the SOI input variable and *D. gigas* catches. The red dashed lines indicate the two standard deviation significance limits.

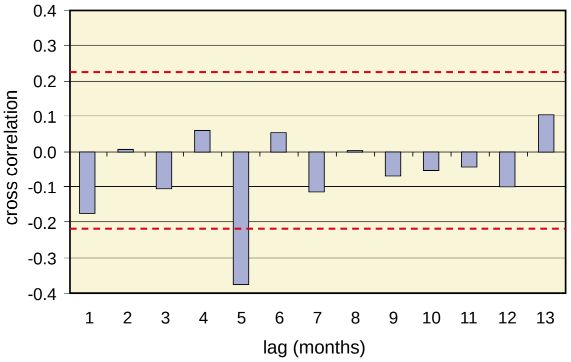

Figure 6. Cross-correlation function for the N1+2 input variable and *D. gigas* catches. The red dashed lines indicate the two standard deviation significance limits.

The mean catch rate of the artisanal fleet off Coquimbo is 3.5 t per trip (up to 7 t per trip), which is higher than those reported by Bojórquez *et al*. (2001) for the Mexican artisanal fleet in the Gulf of California, Mexico, during 1995-1998. On the other hand, Taipe *et al*. (2001) reported mean catch rates of an industrial fleet between 0.7 and 23.8 t per trip off Peru during the 1991-1999 period.

The female jumbo squid captured and measured during the 2006 season off Coquimbo were larger than the males, which coincides for specimens captured as bycatch in identification hauls during acoustic surveys of common hake *Merluccius gayi* in July-September 2002 (Lillo *et al*., 2003) and during July-August 2004 (Lillo *et al*., 2005). According to Nigmatulin *et al*. (2001) and Arguelles *et al*. (2001), the specimens captured in our coasts during the study period should be considered mainly part of the “large” jumbo squid group (> 520 mm ML). The length frequency distribution of specimens captured in Mexico, described by Markaida and Nishizaki (2001, 2003) and Markaida *et al*. (2004), during 1995-1997 period, were significantly smaller than the specimens recorded in this study, and in both cases the females were larger than the males.

Although the values obtained in the analysis using two environmental time series do not indicate strong evidence of a lagged dependency between the processes, one can conclude the existance of causality, which needs to be studied further. Of interest could be to explore longer time series and to correct for the fishing effort associated with the landings.

Acknowledgements

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Use of stable isotopes to examine foraging ecology of jumbo squid (*Dosidicus gigas*)

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Cephalopods are a main prey of many marine predators (including endangered species), and are also voracious predators (Clarke 1983, 1996). Understanding their ecological importance in marine ecosystems has mainly been addressed through the analysis of stomach contents. While such analyses can be quite informative, they have limitations. In this study, we combined stomach content analysis with stable isotope analysis of carbon and nitrogen to investigate the trophic ecology of mesopelagic cephalopods, such as the jumbo squid, *Dosidicus gigas*. We sampled buccal masses and stomach contents of large and medium-sized jumbo squid from three locations in the Gulf of California over three years (see Ruiz-Cooley *et al*., 2006). Muscle samples from their main prey were also collected.

(a) The relationship between mantle length (ML) and both ∂^{13}C and ∂^{15}N values of both muscle and beaks of the jumbo squid were analysed. The results revealed significant differences and high correlations between ∂^{13}C and ∂^{15}N from muscle and beak samples. An ontogenetic effect in trophic position was observed, which was consistent with results from stomach content analysis. The scaling relationships between the isotopic signatures and squid size were as follows ($r^2 = 0.73 – 0.9$; $P<0.001$):

For carbon: ∂^{13}C (muscle) = -17.01 + 0.035 * Mantle length
∂^{13}C (beak) = -17.95 + 0.035 * Mantle length

For nitrogen: ∂^{15}N (muscle) = 13.59 + 0.054 * Mantle length
∂^{15}N (beak) = 9.039 + 0.068 * Mantle length

There was an allometric relationship (slope significantly different from 1.0) between N-isotopic values and squid size, but only a marginally significant relationship (P = 0.06) between C-isotopic values and squid size (Fig. 1).

(b) A comparison of squid tissues revealed that muscle isotopic values were higher than those of beaks by approximately 1‰ for ∂^{13}C and 3.5- 4.0‰ for ∂^{15}N. This C and N-isotopic difference was consistent among all *D. gigas* collected in different years and locations. Therefore, we derived the following equations to estimate C and N isotopic values of muscle using the isotopic signature of beaks:

∂^{13}C (muscle) = - 2.30 + 0.81 ∂^{13}C (beak)
∂^{15}N (muscle) = 7.76 + 0.68 ∂^{15}N (beak)

An open question is whether squid beaks collected from the digestive tracks of their predators can be used to evaluate trophic relationships. We tested this proposition by measuring the C and N-isotopic values of jumbo squid beaks collected from a stomach of a stranded sperm whale, and then comparing these values to the isotopic signatures of *D. gigas* muscle and sperm whale skin (data from Ruiz-Cooley *et al*., 2004). We confirmed viability of this method, at least for jumbo squid in the Gulf of California. More research is needed to investigate the fractionation among squid beak and muscle in other areas.

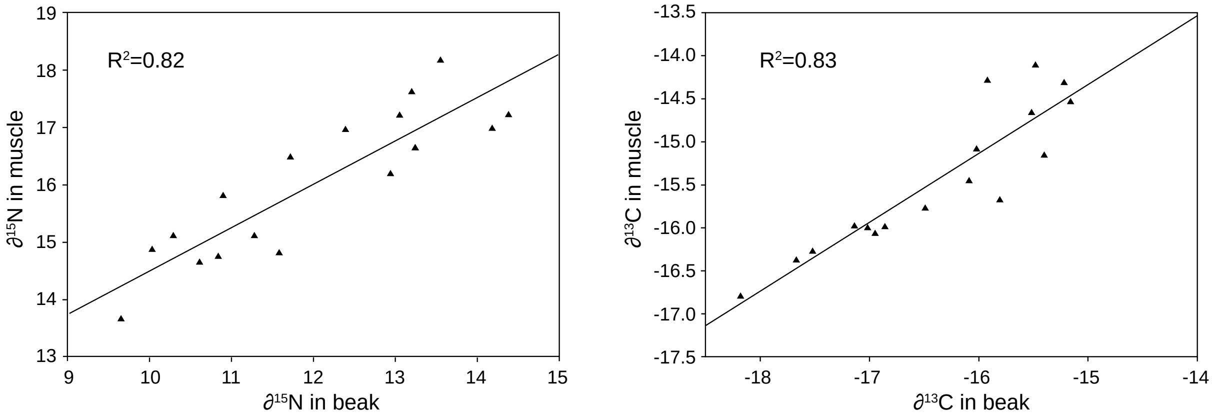

Figure 1. Allometric relationships between stable isotope signatures of beak and muscle tissues of *Dosidicus gigas*. (a) The ∂^{15}N values exhibited significant allometry ($p = 0.002$), while (b) the ∂^{13}C values were marginally significant ($p = 0.06$).

Finally, we compared stomach content analysis versus stable isotope analysis in evaluating squid trophic relationships. Both methods indicated that larger-sized maturing squid showed a higher trophic position than did medium-sized individuals. However, some discrepancies between stomach contents analysis and stable isotope analysis were found. The discrepancies were likely the result of differences between analyses in their respective time frames: stomach content analysis gives an instantaneous estimate of diet, while stable isotope analysis gives an estimate integrated over several weeks. We recommend that tissue samples of prey and predators be collected at the same time and area for a more precise isotopic analysis.

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Signature fatty acids: a robust method for evaluating trophic relationships in open ocean ecosystems

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Introduction

One of the main objectives of CLIOTOP Working Group 3 (Trophic pathways in open ocean ecosystems) is to gather sufficient information on trophic relations of ocean top predators to enable comparisons of the trophic links in the three major oceans. Stomach-content analysis is a traditional means by which trophic relationships may be examined. This approach is limited however, by the absence and/or rapid digestion of food items in the consumers' stomach, particularly for purse-seine caught predators, and provides only a snapshot of daily feeding. Furthermore, the scarcity of studies in the main tropical and temperate oceans (e.g. Indian Ocean) has restricted comparisons between open ocean systems. Therefore, techniques that can provide detailed prey information from the tissues of the predator would greatly contribute to our understanding of trophic connections within and between oceans. Signature fatty acids are showing promise in this area, as once the lipid profiles of a particular prey group are identified they can be used to help elucidate the feeding history of the predator, allowing broad comparisons from relatively few data (Bradshaw *et al*., 2003; Lea *et al*., 2002; Phillips *et al*., 2001; Phleger *et al*., 2005).

Here we report on a pilot study, using signature fatty acids, that examines the contribution of oceanic cephalopods to the diet of broadbill swordfish (*Xiphias gladius*) captured off eastern Australia between July 2004 and August 2006.

Methods

The diet of wild-caught swordfish from eastern Australia was examined through signature fatty acid analysis of swordfish and a range of key prey species, with an emphasis on squid and myctophid fishes. Muscle tissue was collected from swordfish (size range 89-203 cm orbit to fork length) from waters off eastern Australia (Young *et al*., 2006). Samples were extracted and the fatty acids were prepared and analysed by gas chromatography (GC) and GC-mass spectrometry using methods described in Phillips *et al*. (2001) and Phleger *et al*. (2005). The fatty acid compositions (%) comprising 61 fatty acids detected in all species were compared using non-metric multidimensional scaling (MDS) with a Bray-Curtis similarity coefficient (Clark and Gorley, 2006).

Results

Lipid content was moderate in most squid prey (4-10% of dry weight), fish prey (7-9%) and myctophids (6-10%). In contrast, swordfish muscle contained high levels of lipid, 24-42% of dry weight. Levels of DHA (docosahexaenoic acid, 22:6 n-3), a highly reactive PUFA (polyunsaturated fatty acid), when compared in squid from swordfish stomachs, fresh frozen samples, and specimens left at 20°C for 24 hours, were unaffected (Fig. 1). This comparison confirmed the robustness of the signature fatty acid approach, and indicated that stomach-content samples and material not frozen

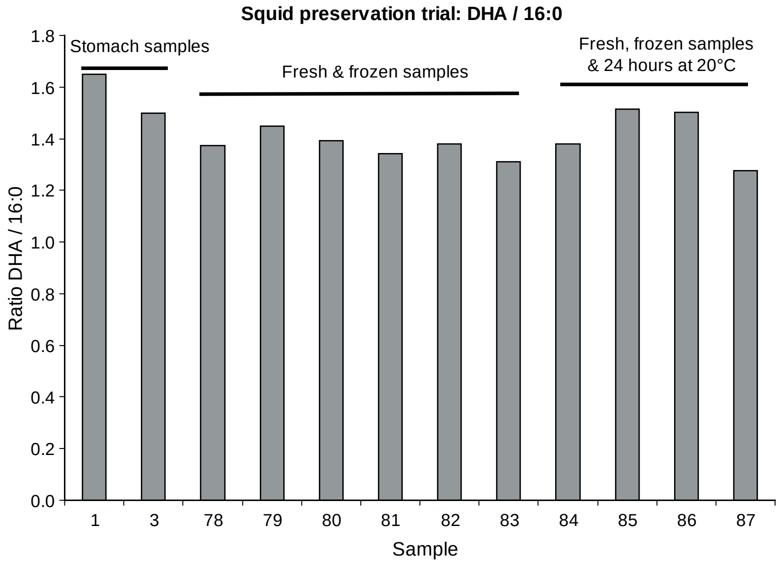

Figure 1. Comparison of the ratio of DHA/16:0 for squid (*Sthenoteuthis oualaniensis*) samples collected and preserved using different procedures.

immediately can still be used when fresh-frozen samples are not available. DHA levels from muscle and skeletal samples dissected from different locations in a whole swordfish also did not show major differences (unpublished data). Whilst sampling from a standardised location along the fish would be the preferred option, where logistic constraints exist and prevent such an approach, these findings also demonstrate that samples from different flesh locations are generally comparable.

Principal fatty acids differed substantially among 24 squid (for example, 34.8% DHA, 10.7% EPA [eicosapentaenoic acid, 20:5 n-3]; Fig. 2) and 20 swordfish (9.7% DHA and 2.0% EPA). Myctophids (40 fish) contained on average 20% DHA and 4.9% EPA, similar to five other fish prey species with 17% DHA and 4.6% EPA. Ordination using multi-dimensional scaling (MDS) indicated that swordfish were trophically more closely related to myctophid fishes (five species) and other fish prey (*Cubiceps baxteri*, *C. pauciradiatus* and *Sudis atrox*) than to seven squid prey species (Fig. 3).

Myctophids, particularly *Diaphus termophilus* and *Ceratoscopelus warmingii*, were also separated by MDS indicating different diets among these prey species. Squid prey species, such as *Sthenoteuthis oualaniensis*, *Ommastrephes bartramii*, *Eucleoteuthis luminosa* and others displayed close trophic affinity, whereas *Argonauta nodosa* and *Todaropsis eblanae* were separated by MDS.

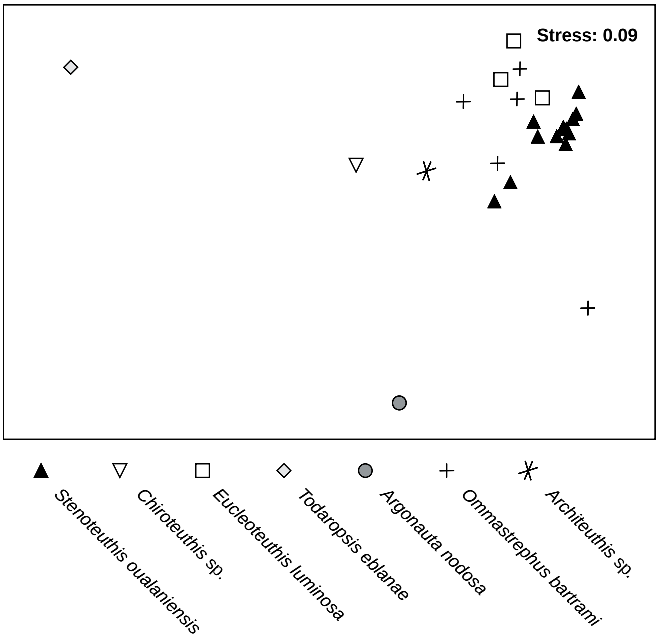

Figure 2. Scatter plot of multi-dimensional scaling (MDS) for fatty acid data (expressed as percent of total fatty acids) of squid. Axis scales are arbitrary in non-metric MDS and are therefore omitted. The data are not transformed or standardised and a Bray Curtis similarity matrix is used.

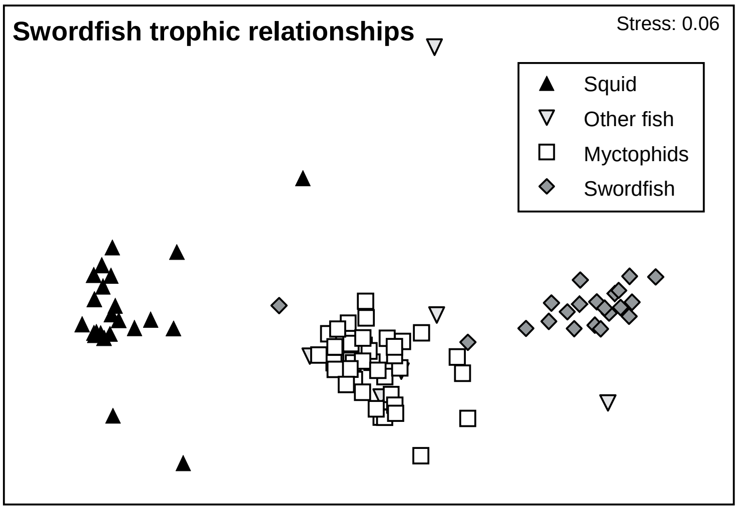

Figure 3. Scatter plot of multi-dimensional scaling (MDS) for fatty acid data (expressed as percent of total fatty acids) of swordfish and potential prey items. Axis scales are arbitrary in non-metric MDS and are therefore omitted. The data are not transformed or standardised and a Bray Curtis similarity matrix is used.

Discussion

Signature fatty acid profiles of a range of myctophid and other fishes grouped these species together. Cephalopod species were clearly distinguishable from all fishes and from the muscle samples of their swordfish predators. The proximity of the myctophid and other fish signatures to the swordfish suggests that fishes were more important as prey than cephalopods, for the swordfish examined. However, the swordfish we examined were nearly all small fish, and we know from recent stomach analyses that small swordfish prey mainly on small fish including myctophids (Young *et al*., 2006). Further sampling of larger swordfish, and from different regions, would help resolve ontogenetic, spatial and temporal variations in their trophic ecology.

Some oegospsid squid species contain oil rich digestive glands (DG), and the FA profiles of the squid DG were similar to myctophid prey (Phillips *et al*., 2001, 2002). As the squid DG lipid is therefore of dietary origin, and the oil content of the DG greatly exceeds that in the mantle, the overall lipid signature of an oegopsid may more closely resemble its prey species than does the lipid in the squid mantle. In this study, the collection and sampling methods used provided squid samples which generally contained only low oil content. Whether or not the squid examined in our study contained lipid-rich DG remains to be investigated.

In summary, signature lipid profiles can be used to complement traditional stomach contents analyses and other biochemical methods, such as stable isotope analysis. Signature lipids have a high potential to increase our understanding of marine predator-prey interactions, particularly for the mid-trophic levels, including cephalopods.

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MODELLING

Assessing the potential role of predation by jumbo squid (*Dosidicus gigas*) and fishing on small pelagics (common sardine *Strangomera bentincki* and anchovy *Engraulis ringens*) and common hake (*Merluccius gayi*) in central Chile, 33-39°S

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Since the early 2000s, jumbo squid (*Dosidicus gigas*) have been unusually abundant off central Chile (33°S-39°S). Although many hypotheses have been proposed for the increase in abundance, there is little agreement on why the increase is occurring. Periodic outbreaks of this species are frequent in central Chile, suggesting some underlying and recurrent cause. Due to the unpredictable nature of these events, there is no fishery for jumbo squid off central Chile, although jumbo squid are occasionally caught by trawlers and purse-seiners that target demersal fishes and small pelagics. Consequently, the biology and trophic ecology of jumbo squid is poorly known in the region.

The jumbo squid is a voracious predator, and this characteristic has been used by Chilean stake holders (from public institutions, fleet owners organisations, workers organisations and some researchers from public and private institutes) to explain the decline in hake (*Merluccius gayi*) (Subsecretaría de Pesca, 2004), and, to a lesser degree, of small pelagic fishes such as the common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*). Here we present results of the trophic impact of jumbo squid on pelagic and demersal fish stocks, particularly the common sardine, anchovy and hake, in waters off central Chile (Fig. 1, Table 1).

We assumed an ecologically sound biomass for this species based on predators and fishery requirements represented in a 31-group Ecopath model of the central Chile marine ecosystem in the year 2000, following Neira *et al*. (2004). With this model, we calculated the biomass of the main prey removed by jumbo squid per year. In addition, using Ecopath with Ecosim (EwE, version 5.1; Christensen and Pauly, 1992; Walters *et al*., 1997), we simulated a one order-of-magnitude increase in the biomass of jumbo squid from year 2000 to 2005. Then, we analysed the effects of this change on the biomass of hake, common sardine and anchovy considering mixed (vulnerability, v=2) and top-down (v=5) trophic controls.

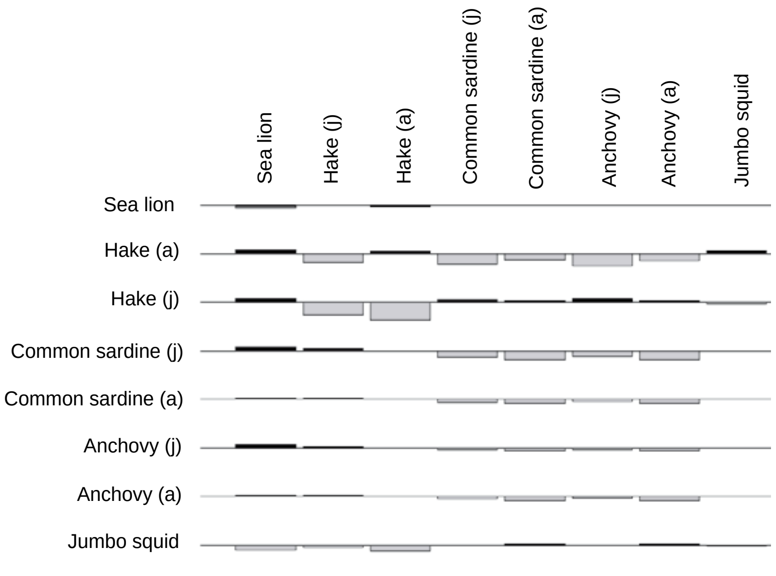

Figure 1. Mixed trophic impacts in the central Chile marine ecosystem, year 2000. Y-axes: impacting groups; X-axes: impacted groups.

Table 1. Inputs and outputs from the Ecopath model representing the central Chile marine ecosystem in the year 2000

Group name	Trophic level	Biomass (t/km²)	P/B (/year)	Q/B (/year)	EE	P/Q
Cetaceans	4.42	0.007	0.600	10.000	0.167	0.060
Sea lion	3.93	0.072	0.250	20.000	0.381	0.013
Marine birds	3.59	0.065	0.500	20.000	0.000	0.025
Hake (juveniles)	3.35	7.793	2.500	8.323	0.977	0.300
Hake (adults)	3.92	12.189	0.456	5.159	0.660	0.088
Common sardine (j)	2.03	41.355	1.453	14.530	0.309	0.100
Common sardine (a)	2.03	14.600	1.875	18.750	0.276	0.100
Anchovy (j)	2.03	23.971	0.703	7.030	0.613	0.100
Anchovy (a)	2.03	14.631	2.120	21.200	0.241	0.100
Squid	3.73	3.337	3.500	10.606	0.999	0.330
Jumbo squid	4.54	6.351	1.750	5.303	0.500	0.330
Mesopelagic fish	3.40	48.985	1.200	12.000	0.999	0.100
Red squat lobster (j)	2.00	0.227	5.900	18.000	0.999	0.328
Red squat lobster (a)	2.00	0.541	3.569	12.500	0.999	0.286
Yellow squat lobster	2.00	0.077	3.569	11.600	0.782	0.308
Shrimp	2.00	0.400	2.500	12.000	0.467	0.208
Horse mackerel	3.52	23.980	0.564	14.200	0.359	0.040
Hoki	3.78	21.900	0.528	5.280	0.992	0.100
Swordfish	4.66	0.640	0.500	5.000	0.750	0.100
Kingklip	3.53	0.300	0.700	3.500	0.351	0.200
Rattail fish	3.00	2.117	0.700	3.500	0.999	0.200
Big-eyed flounder	3.00	0.200	0.700	3.500	0.014	0.200
Cardinal fish	3.50	6.661	0.700	3.500	0.999	0.200
Pacific sand perch	3.57	0.045	0.700	3.500	0.095	0.200
Skates	3.00	0.253	0.362	2.413	0.131	0.150
Polychaetes	2.00	1.886	2.410	15.900	0.000	0.152
Jellyfish	2.63	7.774	0.584	1.420	0.150	0.411
Copepods	2.25	79.257	45.000	154.519	0.999	0.291
Euphausiids	2.50	65.418	13.000	31.707	0.999	0.410
Phytoplankton	1.00	343.713	120.000	-	0.300	-
Detritus	1.00	1000.000	-	-	0.001	-

Additionally, we ran a second simulation analysis using results of an Ecopath model representing the central Chile marine ecosystem in year 1970, that had been calibrated using time series from 1970-2004. Using EwE (Christensen and Pauly, 1992; Walters *et al*., 1997), we simulated the biomass of hake (2005 to 2010), under the following scenarios: a) fishing mortality constant ($F=F_{2005}$); b) F=0 (2007 to 2010). Each fishing scenario was evaluated considering recruitment and predation mortality (constant, 1 variable).

The EwE model estimated a biomass of around 300 thousand tonnes for jumbo squid in central Chile in 2000. Our results showed that jumbo squid had a high trophic level (TL>4), and they could have removed significant levels of biomass of hake, anchovy, common sardine and other prey from the system. However, the analysis did not take into account the varied diet of the jumbo squid.

Specifically, the diet proportions of hake, common sardine and anchovy used in the model were unlikely to reflect the opportunistic predator behaviour of this species. For example, the proportion of hake in its diet was higher than expected from the abundance of hake in the environment. In contrast, small pelagic fishes were relatively under-represented in the diet compared with their abundance in the region.

Simulations with EwE indicated that an increased abundance of jumbo squid from 2000 to 2005 could have had a moderate-to-strong impact on hake biomass, depending on the kind of trophic control simulated (mixed vs. top-down). However, no noticeable impacts were observed for the common sardine and anchovy, regardless of the kind of trophic control simulated.

The dynamics of the hake stock simulated using EwE indicated that the recovery of the stock in the medium- to long-term could be possible only under a F=0 scenario. The effect of predation by jumbo squid on the dynamics of hake was not significant from 2005 onwards.

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The direct and indirect contributions of cephalopods to global marine fisheries

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Cephalopods are a key component of marine food webs, providing sustenance for fishes, seabirds, and marine mammals worldwide. Cephalopods are also of increasing economic importance, evidenced by the rapid rise in their global landings over the past thirty years. Due to their ecological interactions, increased removal of cephalopods from marine ecosystems may have an unintended negative impact on the productivity of their predators, including commercially valuable fish stocks and charismatic megafauna. Thus, increased harvesting could be disadvantageous from both economic and conservation viewpoints. For example, the direct contribution of cephalopods to fishery landings could be less valuable than their indirect contribution through the ecological enhancement of fish production and production of species of non-consumptive value.

We estimated the direct and indirect contribution of cephalopods to marine fisheries in 17 large marine ecosystems (LMEs) using published diet data and species-specific landing and market values (Sea Around Us Project). We also estimated the contribution of cephalopods to two pelagic marine ecosystems, the central north Pacific and eastern tropical Pacific, using previously published data (Ito and Machado, 2000; Cox *et al*., 2002; Olson and Watters, 2003; WPRMC, 2005; FFA, 2006). Our results indicate that, among many of the sampled ecosystems, approximately 10% to 30% of the fishery landings and market values may pass through the cephalopod biomass pool (Figs. 1 and 2). In the Patagonian shelf region, this value may be as high as 50%-55%. As expected, the total contribution (direct + indirect) of cephalopods to fisheries landings is highest in ecosystems in which fisheries are targeting species at the trophic level of cephalopods or higher, i.e. the Patagonian shelf, the eastern tropical Pacific, and the central north Pacific. A similar trend was found for the total contribution of cephalopods to fisheries market values (Fig. 2).

This analysis has identified potential trade-offs among cephalopod and finfish fisheries that should be further evaluated prior to increased expansion of cephalopod fisheries. Additionally, future work should incorporate the conservation value of cephalopods as they are a valuable prey item to species of non-consumptive value and conservation concern.

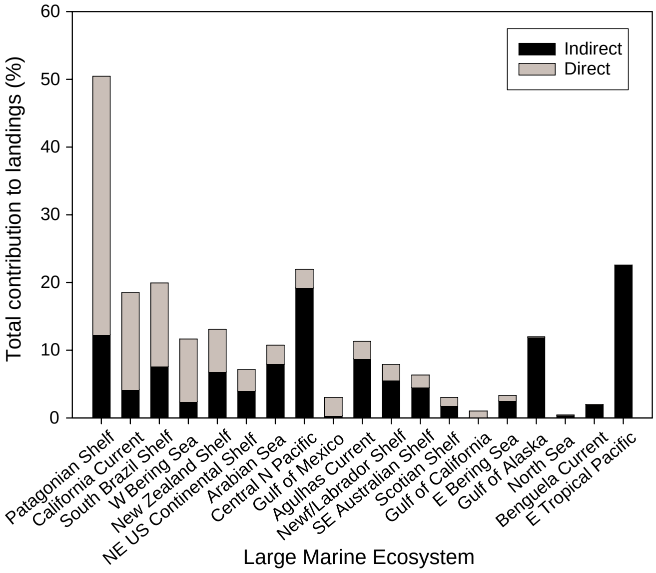

Figure 1. The total contribution (%) of cephalopods to fisheries landings in 19 marine ecosystems. Estimates are based on previously published diet and landings data (LME landings data averaged over years 1990-2001).

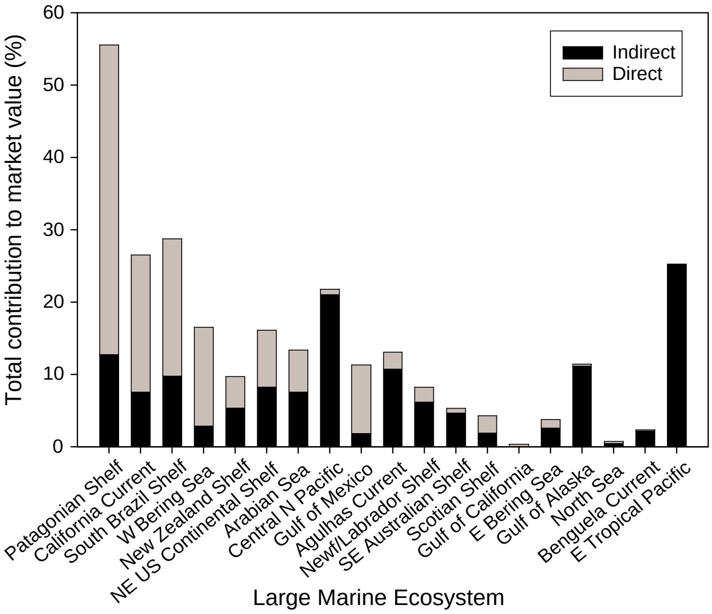

Figure 2. The total contribution (%) of cephalopods to fisheries market values in 19 marine ecosystems. Estimates are based on previously published diet data and market values.

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Modelling environmental influences on squid life history, distribution, and abundance

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Following Caddy and Gulland's (1983) classification, squid populations can be described as displaying irregular or spasmodic abundance fluctuations, as opposed to steady or cyclical patterns. Squid are short-lived, fast growing marine animals, thought to be especially sensitive to environmental influences (Coelho, 1985). Because generations are essentially non-overlapping, modelling of population dynamics reduces to predicting recruitment success (Caddy, 1983; Pierce and Guerra, 1994). Environmental signals are expected to have a strong effect on spawning and hatching success and on growth and survival of early life stages. Since squid are increasingly important fishery resources in many parts of the world, much recent research has focused on understanding their distribution and abundance, to provide the basis for efficient and sustainable utilisation of these resources. The recent high abundance of jumbo squid *Dosidicus gigas* in the eastern Pacific Ocean raises questions as to why abundance and range have increased, the ecological consequences and whether or for how long its current status will persist. The aim of this brief review is to synthesise approaches to modelling the spatiotemporal patterns in squid life history, distribution, abundance and fisheries, and to identify relevant research questions in relation to *D. gigas*.

In principle, models of spatio-temporal variation can be fitted to data on fishery catches and squid distribution, abundance and life history parameters. Critical stages of the life cycle include spawning, hatching, early growth, recruitment to the fishery and movements to the spawning grounds. In many squid, the paralarval (post-hatching) period tends to be the least well known. Because there is no buffering effect of older age classes, environmental effects on the extant generation are a particularly important feature of population dynamics, which has led to a focus on empirical rather than mechanistic models of abundance. In particular, we need to understand the relationship between spawning stock size and subsequent recruitment and pre-spawning mortality of recruits.

Data on squid may arise from fisheries, surveys, predators, tagging or direct observation: all have associated limitations and biases. Relevant considerations include availability, coverage, resolution (in time and space), accuracy and precision. Relevant environmental factors include large scale phenomena such as the *El Niño*-Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO), current systems, fixed physical phenomena such as seabed depth and substrate, oceanographic parameters such as sea surface temperature (SST) and salinity (SSS), meso-scale ocean surface (and sub-surface) features and daily, lunar and seasonal cycles. The selection of relevant variables is normally a compromise between biological relevance and data availability. The most readily available oceanographic data tend to be related to surface characteristics measured by satellite-based instruments, but it is also important to consider the vertical dimension. Developments in remote sensing, geographic information systems (GIS) and statistical modelling have all facilitated current modelling applications.

Empirical modelling is not without its critics: by focusing on the data rather than the underlying mechanisms it encourages data-driven rather than hypothesis-driven research. However, these are also advantages: hypotheses can be generated about the mechanisms and functional forms of relationships. As with all models, adequate testing of predictions is needed to eliminate spurious (coincidental) relationships: as noted by Solow (2002), time-series correlations often disappear once longer series become available, and similar caveats apply to spatial models.

Several generic issues apply to time-series and spatial modelling: these include model selection, model fitting, testing predictions, decisions about scale, incorporating environmental effects that are displaced in space and/or time (time-lags and teleconnections), autocorrelation, seasonal patterns and unexplained trends, interactions between variables, identification of data distributions, variance structure and linearity of relationships.

Time series can be modelled using regression, generalised linear or additive models (GLM or GAM), but such models may be invalidated by temporal auto-correlation, i.e. non-independence of adjacent values of the response variable, which can inflate apparent statistical significance by up to 400% (Zuur *et al.,* 2007). In short-lived species, the link between abundance or life history parameter values in successive generations (years) may be weak or non-existent. In the former case, inserting a term for the previous year's value as an extra explanatory variable into the model may adequately account for autocorrelation. Whether this is an issue can be confirmed by testing the model residuals for temporal autocorrelation. Otherwise, solutions include Generalised Additive Mixed Modelling (GAMM), Seasonal and Trend decomposition using Loess (STL), Autoregressive Integrated Moving Average Models (ARIMA) or Dynamic Factor Analysis (DFA, a multivariate extension of STL). On a cautionary note here, the autocorrelation, moving average, seasonal and trend terms in such models capture variation without explaining it. Environmental parameters may however, be included. Time-lagged relationships with environmental variables can also be detected using cross-correlation analysis; some authors recommend so-called "pre-whitening" (de-trending) of series prior to analysis. However, common trends thus removed may indicate a genuine causal link. Links between *Illex argentinus* abundance and ENSO events, with a 5-year time-lag were detected by Waluda *et al*. (1999).

ARIMA and DFA models of temporal trends in *Loligo forbesi* abundance have been published, and demonstrate effects of SST and the NAO index on abundance (Pierce and Boyle, 2003; Zuur and Pierce, 2004). However, these models tend to have low predictive power and, given the weak temporal structure of the squid time-series, approaches using regression, GAMs or regression trees, may be equally useful (e.g. Bellido *et al*., 2001; Waluda *et al*., 2001). Sims *et al*. (2001) used polynomial regression to demonstrate a link between timing of migration and the NAO index in *L. forbesi*. Pierce *et al*. (2005) used GAMs to extract interannual variation in size at maturity in *L. forbesi*, and then used correlation analysis to demonstrate that this residual variation could be related to the NAO index.

Spatial modelling has been greatly facilitated by GIS (Pierce *et al*., 2002). Routines have been developed to identify meso-scale ocean surface features from variability or discontinuities in temperature (Valavanis *et al*., 2005; Wang *et al*., 2007, see Figure 1), as well as from variability in temperature and chlorophyll anomalies (Valavanis *et al*., 2004a). It is also possible to incorporate temporal variation into such models, although to date, there has been little work modelling distribution in the vertical dimension. Data from tagging have allowed description of squid movements underwater, in relation to oceanographic data, and such data would be amenable to fitting models.

Essential habitat and migration corridor models may be constructed using an entirely GIS-based process, incorporating fishery and environmental data constrained by life history data on species' "preferred" living environmental conditions (Valavanis *et al*., 2002; Valavanis *et al*., 2004b). GAMs have been used to describe distribution patterns in both *L. forbesi* and *I. argentnus*, while regression trees have also been applied to data on *L. forbesi*, revealing relationships with temperature, salinity and depth (Pierce *et al*., 1998; Bellido *et al*., 2001; Sacau *et al*., 2005). Moreno *et al*. (in press) used GAMs to separate seasonal, annual and temperature effects on growth rates in *L. vulgaris*. The latter effects represent spatial variation in growth rates.

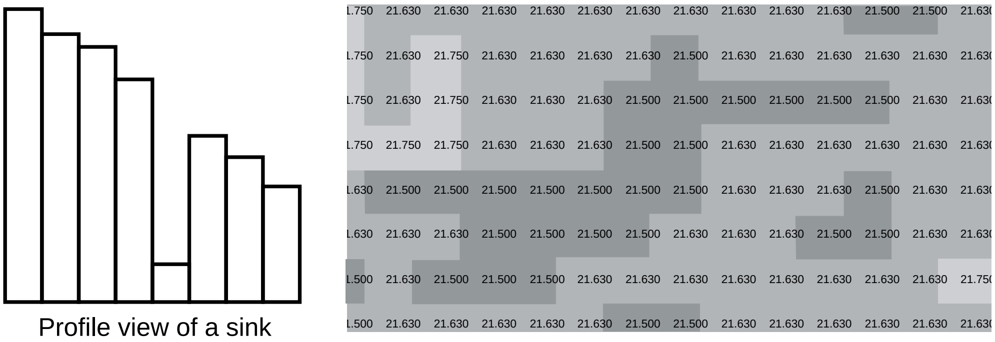
Where presence records are available (e.g. from predator samples or tags) but there are no absence records, presence only modelling techniques such as ENFA (Hirzel *et al*., 2000) may be applied. There are no current applications to data on squid.

2	2	2
2	*i* 2	2
2	2	2

a) Local SST relative variability
RV_i = 1/9 = 0.111

Null	1.1	1.1
1.3	*i* 1.4	1.5
1.6	1.7	1.8

b) Local SST relative variability
RV_i = 7/8 = 0.875



Profile view of a sink

1.750	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.500	21.500	21.63
1.750	21.630	21.750	21.630	21.630	21.630	21.630	21.500	21.630	21.630	21.630	21.630	21.630	21.63
1.750	21.630	21.750	21.630	21.630	21.630	21.500	21.500	21.500	21.500	21.500	21.500	21.630	21.63
1.750	21.750	21.750	21.630	21.630	21.630	21.500	21.500	21.630	21.630	21.630	21.630	21.630	21.63
1.630	21.500	21.500	21.500	21.500	21.500	21.500	21.500	21.630	21.630	21.630	21.500	21.630	21.63
1.630	21.630	21.630	21.500	21.500	21.500	21.500	21.630	21.630	21.630	21.500	21.500	21.630	21.63
1.500	21.630	21.500	21.500	21.500	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.75
1.500	21.630	21.630	21.630	21.630	21.630	21.500	21.500	21.630	21.630	21.630	21.630	21.630	21.63

Figure 1. Use of AVHRR SST data to identify meso-scale ocean surface features. Right: calculating relative variability in SST (Wang *et al*., 2007). Below: identifying SST (and Chla) "sinks" (Valavanis *et al*., 2005).

As with time-series models, autocorrelation in spatial data is an important issue. Model residuals can be checked for spatial autocorrelation, and if none exists, spatial autocorrelation may be ignored. However, ideally, spatial autocorrelation should be included in the model (Pinheiro and Bates, 2000; Wood, 2004; Zuur *et al*., 2007) and this is possible using the software package R, among others. Latitude and/or longitude may be included in models as explanatory variables, although if these effects interact, results will be difficult to interpret. In any case, spatial trends revealed in this way are essentially unexplained trends.

Many of the published models of environmental variation in squid relate to demersal species, in which temperature, salinity and large-scale phenomena (e.g. NAO) have been shown to influence distribution, abundance and life history parameters. While the role of mesoscale ocean surface features was not analysed in these studies, generally because the relevant data were not available, recent analysis has shown that local variability in SST (presumed to be related to fronts) affects hake distribution in the south west Atlantic (Wang *et al*., 2007).

Pelagic squid such as *D. gigas* tend to occur more remotely from land and are less well known than demersal squid. Less dependent on the substrate, they produce many more eggs, with the eggs being pelagic rather than attached to the seabed, hence strongly dependent on currents for dispersal. They tend to be highly migratory and might be expected to show stronger associations with meso-scale ocean surface features and have more variable abundance patterns.

Useful goals for environmental modelling in *D. gigas* would include improved understanding of egg and paralarval distribution, recruitment success and limits to distribution. Tagging data should facilitate 4-dimensional (in space and time) modelling of individual movement patterns. Useful parallels could be drawn from comparative studies on European ommastrephid species such as *Todarodes sagittatus*.

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PERSPECTIVES AND DISCUSSIONS

Squid – the new ecosystem indicators

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Squid occupy most oceanic regions, from the shallow tropical seas to the deep ocean. They play important roles as both predators and prey in these habitats. In many ways, they are ecological equivalents to teleost fishes and compete successfully with them in the various oceanic ecosystems. There is a diversity of body forms in both near-shore and oceanic squid, and their success in the ocean is related to their ability to fill a variety of niches. The large muscular ommastrephid squid (e.g. *Dosidicus*, *Ommastrephes*, *Sthenoteuthis*) play an important role in many ocean current systems, and are formidable predators. These active squid that inhabit the epipelagic realms and function as ecological equivalents to the large piscivorous teleosts, such as the tunas and billfishes. In the near-shore environment, the loliginid squid have life cycles generally associated with shallow water environments and lay their eggs on the bottom and feed on near-shore prey. Loliginids (e.g. *Lolilgo*, *Sepioteuthis*) function much as near-shore finfishes and play an important role in that environment. In the deep ocean, there are large-bodied squid that are ammoniacal, slower moving and probably tend to stalk their prey (e.g. *Mastigoteuthis*, *Moroteuthis*, *Architeuthis*, *Mesonychoteuthis*). These large deepwater squid are functioning as important deep sea predators in much the same way as large sixgill or sleeper sharks do. In fact, squid and other cephalopods may find a refuge in the very deep ocean, where they function as top predators due to the lack of sharks and other elasmobranchs in abyssal waters (Priede *et al*., 2005). Interestingly, while we think of squid as fast moving and generally muscular, there are a number of mesopelagic species that have body cavities full of ammonia and sit within the open ocean like balloons waiting passively to snag prey with their arms and tentacles. There are a variety of cranchiid squid that incorporate this lifestyle (e.g. *Cranchia*, *Liocranchia*, *Teuthwenia*), and they do not swim very much. Such species actually have a life style more in tune with jellyfish than teleosts.

Whatever the strategy adopted, squid are successful components in these diverse environments, although they have a life style that is energetically more costly (jet pressure compared to teleost undulatory swimming, O’Dor and Webber, 1986). In polar waters, ommastrephid squid appear to actually replace large predatory fishes by filling a niche normally occupied by teleosts (Rodhouse and White, 1994). A rapid life style is one feature that stands out for all squid species, as opposed to the majority of larger teleost fishes. Most squid have life spans of less than a year, with few species living beyond a year (Jackson, 1994; Jackson and O’Dor, 2001). Many inshore loliginid species have life spans considerably less than a year, and tropical squid generally have life spans no greater than 200 days (Jackson, 2004). This work has been greatly facilitated by the use of daily statolith growth increments to age squid. This brief lifespan contrasts with that of the majority of large-bodied predatory teleosts that have perennial life cycles, and some deepwater teleosts that can live for over a century.

Squid have thus been referred to as being ‘weeds of the sea’, and living ‘life in the fast lane’. There are a number of features that enable this fast life style: (1) rapid, efficient digestion and a protein-based metabolism that converts food into growth rather than storage, (2) continual recruitment of new muscle (hyperplasia) fibres throughout growth, (3) efficient utilisation of oxygen and (4) low levels of antioxidative defense (Jackson and O’Dor, 2001). These features enable the rapid growth and short life spans of squid. They also drive the continual non-asymptotic growth that is a common feature of squid, and very different to the asymptotic growth of teleost fishes. The continued recruitment of new muscle fibres throughout the life cycle is thought to be one of the physical mechanisms that

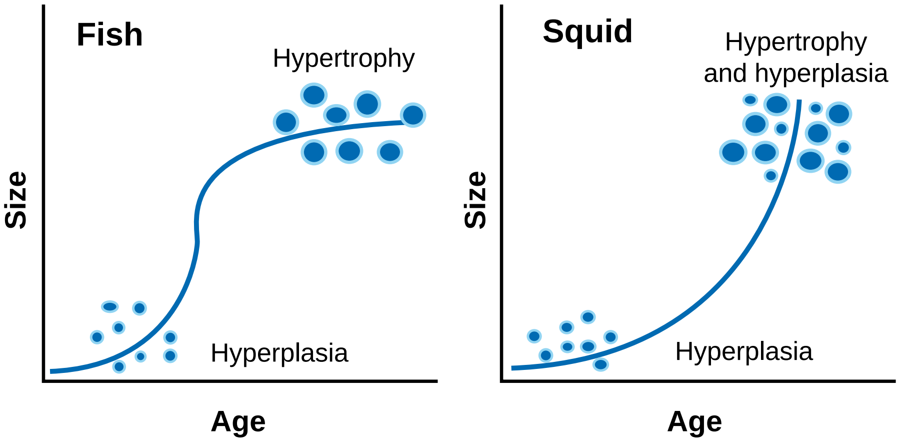

Figure 1. Diagrammatic representation of asymptotic growth of fishes, in which hyperplasia ceases and growth only occurs by hypertrophy, compared with non-asymptotic continual growth in squid, which show both hypertrophy and hyperplasia in adults. The circles on the graph represent the relative sizes of muscle fibres.

enable the rapid continual growth of squid (Moltschaniwskyj, 1994). In contrast, while teleost fish have hyperplasia when young, this eventually ceases later during ontogeny, and fish are dependent on enlargement of existing muscle fibres to drive growth (Fig. 1).

Fast growth rates and short life spans in squid result in a rapid turnover of populations. This makes managing squid fisheries challenging and predicting potential recruitment almost impossible. Squid populations appear to be more influenced by oceanographic conditions rather than by fishing pressure, and stock fluctuations appear to be closely tied with environmental conditions (Waluda *et al*., 2004). Squid also have huge biomass. It has been estimated that a single predator, the sperm whale consumes annually 100 million tonnes of squid per year. This value is similar to all world fisheries catches combined and equates to about the half the biomass of humanity (Clarke, 1980). Although the biomass is high, given the rapid life spans of squid, there is a rapid turnover in biomass over time. During times of food shortages, squid readily turn to cannibalism, which can also act to limit biomass.

The fast life style of squid means that they have extremely plastic growth, depending on existing environmental conditions. Growth rates and body size can change rapidly if thermal or biological conditions markedly change over short time periods. This was reflected in the population of *Loligo opalescens* off the California coast (Jackson and Domeier, 2003). Individuals of *L. opalescens* that lived through the 1997 *El Niño* had substantially smaller body sizes and slower growth rates compared to individuals that grew through the subsequent *La Niña* period, which was cooler but dramatically more productive, with increased upwelling and zooplankton. Thus, the population parameters of squid will quickly respond to the conditions that they experience, providing a means to monitor changes within the marine ecosystem. Due to the fast life styles of squid, they can act as real time ecosystem indicators and productivity integrators. Longer-lived organisms cannot monitor the environment in this way, as longer life spans and slower growth rates mean that environmental changes are integrated over much longer time periods. Although we now have relatively synoptic data on ocean climate itself, we still do not know how to translate this into edible biomass.

Collecting long-term time series of squid age and growth in relation to oceanographic data can thus serve as a means to monitor how key elements in the marine community respond to ongoing changing environmental conditions. As the marine environment faces global warming and increasing sea temperatures, it is likely that nearshore and shallow water squid populations will be one of the first organisms to reflect changes in a new warmer marine environment. Because squid play important roles in a variety of marine ecosystems, and because they are commercially important, changes in squid populations will probably lead to a variety of profound effects.

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Perspectives on *Dosidicus gigas* in a changing world

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Overview

A large portion of "The Role of Squid in Open Ocean Ecosystems" workshop was focused on one species of oceanic squid – *Dosidicus gigas* (Humboldt or jumbo squid), the largest member of the family Ommastrephidae. Furthering our understanding of this species and its interactions with the ecosystems in the eastern Pacific Ocean was deemed to be of critical importance for reasons discussed below. Many of the features of *D. gigas* biology are likely to be relevant to other ommastrephids in the eastern Pacific, particularly *Sthenoteuthis oualaniensis* and *Ommastrephes bartramii*, which have overlapping ranges, are genetically close and probably show similar behaviours (Nakamura, 1993; Nesis, 1993; Yokawa, 1994).

Because of its extremely fast growth, highly migratory nature and profound adaptability, *D. gigas* (and probably other ommastrephid species) are likely to provide a rapid indicator of environmental changes on a spatial scale ranging from local to whole ocean basins. The invasion of *D. gigas* into new areas is undoubtedly related, in specific ways, to oceanographic changes that alter productivity, e.g. temperature, upwelling, oxygen levels, etc. As discussed below, many mesopelagic organisms on which *D. gigas* feed are short-lived species that can also respond quickly to environmental perturbations and productivity events. Unfortunately, our knowledge of the dynamics of responsiveness of either squid predators or their prey to environmental fluctuations is presently limited, and improving this situation should be given high priority in directing research efforts.

If *D. gigas* reacts rapidly to take advantage of perturbations, its appearance provides a positive indication of climate change. Sometimes such indications can be extremely dramatic, such as mass strandings of large squid visible to even the most casual observer. In general, appearance is a much less ambiguous and more easily monitored signal than the disappearance or inhibition of a 'standard' indicator species. Additional research that is aimed at providing a deeper understanding of migrations by *D. gigas* would provide the basis for interpreting the relationships of movements to particular oceanographic or food web variables. The tight coupling between *D. gigas* and its prey, and the adaptability of both groups, lies at the heart of what we need to know, and we will have to learn more about both to elucidate any overall principles. It is already becoming apparent that *D. gigas* may be exerting a strong top-down predatory influence on the pelagic ecosystems that it invades, and this restructuring may act to amplify and modify impacts of climate change on many prey species in complex ways that would not be predicted from direct effects of climate change alone.

This article is not intended to be a comprehensive review of the biology of *D. gigas*. Instead, we focus on aspects that we feel are most relevant to climate change. We also propose an outline for a research programme that would greatly expand our view. A large part of this research could be immediately carried out with established methods – what is needed is a systematic, large-scale study in both northern and southern hemispheres. In addition, some newer methodologies should be adapted for use with *D. gigas* and other ommastrephid squid. Development of these techniques must be encouraged, and they would provide a strong complementary set of tools to methods already established. It seems clear that studies today about pelagic food webs that are expanding and thriving in response to climate change will provide insight into what the oceans will look like in the future. We do not know the distance to the future, but it is likely we are already well on the way.

Why is *Dosidicus gigas* ecologically and economically important on a global scale?

A number of factors come together and reveal the importance of *D. gigas*, 1) large geographic range, 2) enormous biomass and extremely high reproductive output, 3) flexible feeding strategies, 4) tolerance of environmental extremes, and 5) great fishery potential. These factors are discussed individually below.

1) Expanding range. *D. gigas* is a highly migratory oceanic squid that also inhabits continental shelf environments. It differs in this latter regard from *S. oualaniensis* and *O. bartramii*, both of which are more truly oceanic. *D. gigas* has an enormous historical range in the eastern Pacific, stretching from central California to northern Chile (Roper *et al*., 1984; Nigmatullin *et al*., 2001). During the last few years this range has expanded to Alaska (Cosgrove, 2005; Wing, 2005) and southern Chile (Chong *et al*., 2005). Although the western boundary for the species is thought to be about 140°W at the equator (Wormuth, 1998), this longitude is rather vague. It is not known whether westward expansion is also occurring.

Such range expansions can be long-lasting or transient, but our understanding of the reasons for such expansions, including underlying oceanographic perturbations, is very incomplete. Satellite tagging studies in the Gulf of California have revealed that individual jumbo squid undertake daily horizontal movements of tens of km, even at times when no mass directed-migrations are known to be occurring (Gilly *et al*., 2006b and unpublished data). This short-term migratory behaviour is probably associated with searching for food and is likely to be intimately related to the nature of *D. gigas* as a species to undertake periodic excursions (Gilly, 2005).

2) Biomass and reproductive output. Presently, there is no good estimate of the biomass of *D. gigas*, but analysis of stomach contents of sperm whales in Peru before the curtailment of commercial whaling indicated that sperm whales alone consumed about 10 million tonnes of *D. gigas* each year off Chile and Peru (Clarke *et al*., 1988). Clearly the biomass is extremely large, and may be increasing along with geographical range.

Dosidicus gigas is the most fecund of all cephalopods, producing up to 30 million eggs per female (Nigmatullin *et al*., 1999). Growth is extraordinarily rapid, with a tiny planktonic hatchling of ~0.01 g (unpublished data; Yatsu *et al*., 1999) reaching an adult size of 40 kg or more in a life-span of only 1-2 years (Arkhipkin and Murzov, 1986; Masuda *et al*., 1998; Markaida *et al*., 2004). *D. gigas* also shows a complex population structure, with a high degree of variability in the size reached by an individual animal at the time of sexual maturity (Nigmatullin *et al*., 2001). This plasticity appears to be related to environmental factors, including temperature and food supply (Nesis, 1983; Markaida *et al*., 2004; Bazzino *et al*., 2007).

Altered size-structure of *D. gigas* populations by climate change would be expected to lead to a complex suite of ecological impacts. Juvenile jumbo squid serve as prey for many species of pelagic fishes, including tunas, billfishes and seabirds throughout the squid's range (Perrin *et al*., 1973; Pinkas *et al*., 1971; Abitia-Cardenas *et al*., 1999; Olson and Galván-Magaña, 2002). Large adults serve as prey for the largest fishes, such as swordfish (de Sylva, 1962; Ibáñez *et al*., 2004; Markaida and Sosa-Nishizaki, 1998; Markaida and Hochberg, 2005), and marine mammals, including sperm whales both off Peru (Clarke *et al*., 1976, 1988; Fiscus *et al*., 1989) and in the Gulf of California (Jaquet and Gendron, 2002, 2003; Ruiz-Cooley *et al*., 2004, 2006). Thus, different predators will be selectively impacted, either positively or negatively, by environmentally influenced changes in the body size of jumbo squid available to them in a given area.

3) Feeding strategies. *Dosidicus gigas* is a voracious, opportunistic predator that consumes vast quantities of mesopelagic myctophid fishes, crustaceans and other cephalopods, including its own kind (Markaida, 2006; Markaida and Sosa-Nishizaki, 2003; Shchetinnikov, 1986, 1989), thereby directly competing with pelagic vertebrates that also forage on these organisms. But these feeding habits also mean that *D. gigas* provides an important and direct link between small mesopelagic organisms and apex vertebrate predators. The relationship of *D. gigas* to vertebrate predators is thus, an extremely complex and multidimensional one.

Most of our knowledge concerning the diet of *D. gigas* comes from work in the Gulf of California. Recent stomach-content analyses from the Pacific Ocean, both off Magdalena Bay (Baja California Sur, Mexico) and off central California were presented at the meeting by Unai Markaida and Ken Baltz, respectively. Both studies revealed substantial differences from the diets described in the Gulf, particularly in greater numbers and variety of larger, neritic fishes. This finding was especially dramatic in the California case, in which *D. gigas* was found to be preying on commercially valuable fishes, including hake and rockfishes (Field *et al*., in press). *D. gigas* has also been implicated with reductions of hake populations in Chile (Ibáñez and Cubillos, in press; Arancibia and Neira, p.68 this volume) and with predation on yellowfin tuna during commercial fishing operations (Olson *et al*., 2006). Although little is known about predatory behaviour directed against such larger fish species, adult jumbo squid are clearly physically capable of preying on large fishes.

Feeding habits of *D. gigas* are thus extremely diverse. Perhaps most importantly, flexibility in foraging strategies allows jumbo squid to take maximum advantage of whatever prey resources they encounter in the course of their migrations.

4) Environmental tolerance. Archival electronic tagging of *D. gigas* in the Gulf of California has revealed that the squid can move frequently over the course of a day between near-surface waters, which are well oxygenated (cool in winter, hot in summer), and cold, deep waters of 300 m or more, which can be seriously hypoxic (Gilly *et al*., 2006b). Remarkably, the squid appears to be highly active in both environments and may forage continuously. Tolerance of such environmental extremes, coupled with a flexible diet, would clearly be advantageous to *D. gigas* when it ranges into a new and unfamiliar area, as in the case of its recent northward range expansions

Unpublished tagging results also suggest that *D. gigas* varies its behavioural patterns, presumably reflecting foraging strategies, seasonally in the Gulf of California. In this region, sea-surface temperature, prevailing winds and currents, productivity events (upwelling), as well as the oxygen profile of the water column all show dramatic seasonal changes. Thus, *D. gigas* is well adapted to major environmental changes on a regional scale. How this adaptability extrapolates to other areas in its broad range is unknown, but it is again likely to be a major factor in periodic excursions and longer-lasting range expansions.

5) Fishery. *Dosidicus gigas* presently supports the world's largest cephalopod fishery – 800,000 tonnes in 2004 (FAO statistics), primarily from Chile, Peru and Mexico. It constitutes the third most valuable fishery in Mexico, with typical landings of 100,000 tonnes made almost entirely in a small near-shore portion of the Guaymas Basin in the Gulf of California. Recently, landings have expanded elsewhere in Mexico, particularly off Magdalena Bay on the Pacific coast of Baja California, where a fishery has developed in the springtime.

Perhaps an equally important factor concerning fisheries relates to potentially negative impacts of *D. gigas* invasions on established commercial and recreational fisheries. As discussed above, such impacts are probably occurring at the present time in the California Current system (Field *et al*., in press; Zeidberg and Robison, 2007) and elsewhere. At the present time, recreational fisheries in southern California are being heavily impacted by *D. gigas* (Thomas, 2007; Sarabia, 2007).

Taken together, these characteristics indicate that *D. gigas* is ecologically important as both predator and prey over much of the eastern Pacific. Moreover, they strongly suggest that *D. gigas* plays a major role in structuring the pelagic and mesopelagic ecosystems in this large region, particularly in areas that it invades. *D. gigas* can cope with large variations in temperature, dissolved oxygen levels, and prey type. It is highly migratory and can react rapidly to environmental changes on a variety of temporal and spatial scales. Changing climate conditions, due to both natural and anthropogenic factors, will undoubtedly lead to future alterations of the range of *D. gigas* and its relationships to food webs that connect fishes, seabirds, marine mammals and humans.

What more do we need to learn and where do we look?

All of the aspects reviewed above led to an informal consensus at this workshop that an international research effort was immediately needed to advance our knowledge of *D. gigas* and its impacts on the highly productive ecosystems in its range, including the California and Peru Currents and the Costa Rica Dome. Because of the present range expansion, it was deemed that such research should be carried out as rapidly as possible because of the window of opportunity. In many cases, necessary research methods are already in use and have demonstrated feasibility. These efforts should commence immediately. In other cases, adaptation of newer methods will be necessary, and rapid developments in this area should be encouraged.

Because of the large geographic range of *D. gigas* and the substantial regional ecological differences, it would seem necessary to approach the problem by dividing the species range into bio-geographical regions, each with a coordinating investigator and specific participants. These should include: 1) Pacific Northwest (Alaska, British Columbia, Washington, Oregon), 2) California, 3) Mexico (Gulf of California and Pacific Ocean), 4) Costa Rica Dome and Ecuador, 5) Peru, and 6) Chile.

A variety of proven methods should be used to address the questions outlined below, with a consistent programme applied across the 6 regions. It seems likely that we will be able to elucidate general truths only by systematically comparing results from the same approaches in different regions. New methods must be developed and added to the programme as their feasibility is demonstrated. Such a programme must be comprehensive to succeed. Variability and flexibility are key features of *D. gigas* that make it successful, and this must be kept in mind when designing a coordinated research effort that must search for common threads in data from different regions collected by different investigators.

Identification of specific model-systems that support quasi-stable populations of *D. gigas* on a year-round basis should be particularly encouraged, because intense, focused study in such areas is tractable and likely to reveal important links between environmental signals and squid movements that are applicable on much larger geographic scales. In the Guaymas Basin of the Gulf of California, a fairly well-defined seasonal movement of *D. gigas* occurs between summer fishing grounds on the Baja coast and winter grounds off the mainland coast in Sonora (Markaida *et al*., 2005). In the Monterey canyon system off central California, *D. gigas* appears to be present year-round but is more abundant in the winter (Zeidberg and Robison, 2007). A large scale migration pattern centred on the Costa Rica Dome has been proposed for South American waters (Nesis, 1983), but no direct demonstration has been made.

In no case, do we yet understand the relationship between environmental or oceanographic events and squid movements, and a close examination of these data sets needs to be undertaken. Identification of other geographically restricted areas with well-defined annual movements of squid would be valuable. Such areas, particularly in the southern hemisphere, might be identifiable simply from local commercial landings data. Focused study of these sites should be encouraged.

What general questions can be studied with existing methodology?

1) Where are the squid at any given time? This includes analysis of horizontal migrations and their progress over both short- and long-term time scales. These movements should be viewed in association with seasonality and oceanographic conditions, especially productivity, temperature, and dissolved oxygen. Methods available include jigging surveys, conventional tag-and-recapture studies, acoustic tracking using the POST array in the Pacific Northwest, and pop-up satellite-tag methods.

All of these approaches should be complemented by an analysis of the available satellite data and with conventional oceanographic profiles collected in the field. In particular, oxygen-depth profiles should be sampled more often and at more selected locations in some coherent manner. Available data should be compiled and changes over time examined – for example in relation to the appearance of *D. gigas* in the Gulf of California (pre 1970?), Monterey Bay (post 1997/98 ENSO) or Alaska (2004). The nearshore hypoxia anomaly off Oregon (Grantham *et al*., 2004) during the recent spread of *D. gigas* through the Pacific Northwest is a good example of such a candidate event.

Development of new methods, such as analysis of statolith microchemistry to determine geographical migrations, should be encouraged. Examining how the population dynamics of *D. gigas* varies across the range of its habitat, using statolith ageing and possibly gladius (pen) increment analysis, would shed light on population turnover rates, and this information is necessary for developing ecosystem models relevant to the different climatic zones where *D. gigas* is found.

Sampling *D. gigas* and other ommastrephid squid using research driftnets from the coast to offshore, similar to the manner in which Ichii *et al.* (p.31 this volume) studied *Todarodes pacificus*, would shed much light on changes in geographical range of a given species. For example, what is the western boundary of *D. gigas*? What is the habitat separation/overlap between *D. gigas* and other ommastrephid species in the Pacific?

2) Where and when does breeding occur? The Costa Rica Dome area was thought to be the major spawning ground (Vecchione, 1999), but recent work in the Guaymas Basin suggests that spawning takes place there as well (Gilly *et al*., 2006a). It seems likely that other (perhaps many other) spawning areas exist (Nesis, 1983; Nigmatullin *et al*., 2001). Conventional plankton tows for *D. gigas* paralarvae or dip-netting small juveniles at the surface at night are good indicators of recent spawning in a general area. In many areas of the eastern Pacific, standard genetic analysis of ommastrephid paralarvae will be necessary to unambiguously identify the species collected (Gilly *et al*., 2006a) because of overlap with other ommastrephid squid, particularly *Sthenoteuthis oualaniensis* and poor morphological differentiation to species level despite previous efforts working with paralarvae (Camarillo-Coop *et al*., p.7 this volume; Granados-Amores *et al*., p.22 this volume; Yatsu *et al*., 1998).

An historical examination of this question might also be possible by identification of *D. gigas* paralarvae and juveniles in available zooplankton samples from previous studies, such as the CalCOFI sampling of the California Current system (Okutani and McGowan, 1969). Other sampling programmes in Mexico and the southern hemisphere may also have yielded useful collections, and these need to be systematically examined.

3) Do genetically identifiable populations exist? Recent genetics work, using a RAPD approach (Sandoval-Castellanos *et al*., 2007) as well as analysis of mitochondrial gene sequences (our work, in preparation) has revealed little spatial structure for *D. gigas* populations over a broad geographical scale. Future work directed at this important question should include development of additional genetic markers, including microsatellites.

4) What are the squid eating as adults and juveniles? What vertebrate species are eating them at different stages? How variable are these links and how rapidly do they change? Traditional gut-content analysis of adult and juvenile squid, as well as vertebrate predators, would go a long way to answering these questions. Application of newer methods, as discussed below, would also be extremely helpful.

5) What are the characteristics of short-term vertical migrations, i.e., how are squid utilising the water column? This question is intimately linked to diet, because *D. gigas* undoubtedly employs vertical (as well as horizontal) migrations to search for optimal foraging areas. We have been observing much individuality in both dynamics of vertical migrations and diet in the Gulf of California, and it will be important to sample enough individuals to obtain a general picture at any one place and time. Archival electronic tags can be used in areas with high levels of commercial fishing, and fishery-independent pop-up satellite-tag methods can be employed anywhere (Gilly *et al*., 2006b). At present there is no commercially available tag that is capable of measuring dissolved oxygen at the depths inhabited by *D. gigas*. Development of such a tag would provide a powerful new tool, because of the strong link between this squid and hypoxic midwater environments.

6) How many squid are being caught commercially – where and when? Historical and contemporary commercial landings data provide a good indicator of the presence of squid and a detector of range expansions. Analysis of such data in conjunction with satellite and oceanographic data bases might provide valuable insights into reasons underlying long-term range expansions (Waluda *et al*., 2004; Waluda and Rodhouse, 2006).

7) What are the local social and economic effects of the squid fishery? Although *D. gigas* is presently the target of the world's largest cephalopod fishery, much of the fishing (in both the northern and southern hemispheres) is artisanal in nature and carried out in small vessels. In some cases, such as Santa Rosalia in the Gulf of California, a large part of the local economy depends on the squid fishery, either directly or indirectly. Impacts of this fishery on such local communities are important to document, because they are part of the relevant ecosystems, and must ultimately be considered in any management plans for marine resources. Development of the *D. gigas* fishery has historically depended on demand from Asian markets. This makes for volatile local squid prices and a risky fishery.

8) What kind of models can be developed for fast-growing, short-lived squid and their reactions to environmental perturbations and climate change? This issue is discussed by Graham Pierce (p.73 this volume). Although we are still lacking much of the biological data to guide modelling, application of established fisheries models, based on long-lived species like fishes, are unlikely to accurately account for or predict variations in squid abundance or distribution. This will be a challenging and ultimately rewarding area for research.

Newer methodologies

A number of relatively recently developed techniques have been applied to other squid species, and need to be adapted or validated for use with *D. gigas* and other ommastrephid squid. Numbering of this section corresponds to that above.

1a) Analysis of migrations through statolith microchemistry. Seasonal collection of samples of *D. gigas* paralarvae should be made wherever they are available (especially in the Gulf of California and Costa Rica Dome), and the extracted statoliths should be used for microchemical analysis to obtain an elemental fingerprint of home regions using ICPMS. Analysis of statoliths from adults collected along expansion fronts, or elsewhere, could then determine the fingerprint of the central-most (oldest) region to detect the natal hatching region. This technique has been successfully used for defining hatch regions for a reef squid, *Sepioteuthis australis*, in Tasmania by Gretta Pecl, University of Tasmania, but early work on an ommastrephid, *Ommastrephes bartramii*, proved not to be so successful (Yatsu *et al*., 1998). Recent progress in this field is encouraging, and application to oceanic squid clearly needs exploration.

1b) Dynamics of movements of individual squid using acoustic tags. Acoustic tagging technology should be applied in conjunction with the extended acoustic array being developed by POST and OTN in the northern hemisphere. Important predators, such as sperm whales in the Gulf of California, should also be tagged in order to track their movements. Strategic VR3 acoustic receivers can be placed at the entrance and within the Gulf of California to expand the geographical extent of the existing POST array. The existing POST array would be able to track the movement of *D. gigas* as individuals move between California and Alaska.

1c) Use of acoustic (sonar) technology to monitor squid movements and estimate biomass. Although squid generally are thought to be problematic targets for acoustic surveys, the large size of *D. gigas* and relatively simple structure of the midwater community in certain areas where it is abundant, e.g. Gulf of California (relatively simple) vs. California Current system (much more complex), makes application of these methods promising. Recent preliminary field trials in the Gulf of California were extremely encouraging (Benoit-Bird *et al*., submitted). Development of acoustic methods for biomass estimation should be a high priority research goal, because such data are necessary for both a deeper understanding of the ecology of the species and for any management measures. Because acoustic methods can be applied over a relatively large area in a small amount of time, they would be excellent in limited regions where *D. gigas* is abundant, for example the Guaymas Basin. Real-time acoustic monitoring of squid in the water column would also provide an independent means of studying how *D. gigas* utilises the water column in relation to acoustic scattering layers and other oceanographic features.

2) Utilisation of existing samples to map presence of paralarvae. Documenting the historical presence of *D. gigas* in the California Current should be feasible through identification of paralarvae in zooplankton collections made by previous CalCOFI expeditions or by similar programmes in Mexico (IMECOCAL) and in South America.

3) Fatty acid and stable isotope analysis of trophic linkages. Application of these techniques should be encouraged to better understand the prey of *D. gigas* using signature fatty acid analysis and stable isotope analysis (Ruiz-Cooley *et al*., 2006). Sampling needs to be carried out on thoughtful spatial and temporal scales. Sperm whale blubber biopsies can be collected for comparing the fatty acid and stable isotope signatures between these important predators and prey. In the Gulf of California, consumption of *D. gigas* by sperm whales is probably on the order of that landed commercially – about 100,000 tonnes per year. Again, this factor is relevant to both basic ecology of the species and in management efforts, and any management plan must account for potential impacts of the squid fishery on marine mammal populations (Clarke *et al*., 1993).

4a) Development of an oxygen-sensing archival tag. Because of the strong link between *D. gigas* movements and the midwater hypoxic environment presented by the oxygen-minimum layer (OML), efforts to commercially develop an archival tag that also samples oxygen to depths of 1,000 metres should be encouraged. Such tags would also be extremely valuable for studying other species of ommastrephid squid and pelagic predatory fishes, especially tunas, in the eastern Pacific. These fishes must be limited in their ability to forage in the OML, and *D. gigas* is likely to be the top predator in this vast midwater environment (excluding marine mammals). Utilisation of the OML may be one of the most important biological features of *D. gigas*, but the present inability to directly relate archival data of vertical and horizontal movements to oxygen levels measured simultaneously is a major limitation.

4b) Understanding the mesopelagic community through new technologies. In order to truly understand how *D. gigas* utilises the water column, we will have to learn much more about the other organisms that it interacts with at various depths and times. Clearly, *D. gigas* depends heavily on the mesopelagic micronektonic community on which it feeds. Even though much of the productivity in the eastern Pacific is channelled through this community, dynamics of the energy transfer through this system remain poorly understood. This community is characterised by short-lived (often annual) organisms whose productivity is larger than their standing stock. Such organisms tend to respond quickly to environmental variations, and these responses are likely to be intimately related to historical variations in *D. gigas* abundance and distribution. Large historical variations are characteristic of scale deposition by myctophids in the deep-basin sediments in the Gulf of California (Holmgren-Urba and Baumgartner, 1993), but this feature has not been well exploited as a tool in studies of midwater ecology.

Understanding the community of micronektonic fishes, squid and crustaceans has proven difficult, largely due to major challenges involved in systematic and large-scale sampling efforts, but also due to small-scale problems inherent with net sampling, particularly net avoidance by reactive organisms. Perfection of newer techniques, including acoustic surveys and low-light cameras, promises to greatly aid future research (Benoit-Bird and Au, 2006).

Studying dynamics of mesopelagic planktonic communities will be challenging and expensive, but failure to advance in this area will almost certainly preclude achieving a deep understanding of environmental changes and how they are impacting top pelagic predators. The relevant organisms, like myctophids, may be difficult to study and not particularly charismatic, but they really matter. We are reminded of a dictum made by Steinbeck and Ricketts in Sea of Cortez (1941) - “None of it is important or all of it is.”

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