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**The Cephalopod *Dosidicus gigas* of the Humboldt Current System Under the Impact of Fishery and Environmental Variability**

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Dissertation zur Erlangung des akademischen Grades  
Doktor der Naturwissenschaften (Dr. rer. nat.)

vorgelegt am Fachbereich 2 (Biologie/Chemie)  
der Universität Bremen

im April 2009



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to the commonality of humankind  
and to those who not forget it



## Acknowledgements

I want to thank all people that contributed to the successful completion of this work. Primarily and in first place I have to thank Matthias Wolff who not only helped to finish this project but also contributed a great deal that it took off. In Peru I want to thank all colleagues and friends at IMARPE that welcomed me in the first place and helped me ever after: Juan Argüelles, Sara Purca, Ernesto Fernández, Ricardo Tafur, Michael Ballón, Anatolio Taipe, Carmen Yamashiro, Ana Alegre, Michi Graco, Pepe Espinoza, Claudia Wosnitza, Juan “del Diablo” Rubio, David Correa, Jorge Tam, Octavio Morón and Carlos Benites. I want to thank Renato Guevara, the then and now scientific director of the IMARPE who with a simple email left me no choice but to aim my doctorate project to the pota. Thank goes to the numerous onboard observers of IMARPE in the industrial jig fisheries that collected most of the data that was the basis of my thesis. I want to thank especially my piscologist Jaime Mendo. In Chile I want to thank Pedro Pizarro and all colleagues at the UAP of Iquique, Lucho Cubillos and all colleagues at the UC, Maria Cecilia Pardo and of course Christian “la pota es Chileno” Marcelo Ibáñez, a friend and colleague as there is no other... In Galapagos I want to thank Diego “pulpo” Ruiz, Annika Krutwa, Stuart Banks and all other colleagues at the CDRS. In Germany my thanks go to my colleagues at the ZMT and the Universität Bremen: Karen Diele, Marie Badjeck, Flora Vadas, Alejandro Espinoza, Jorge “el Horge” Paramo, Hauke Reuter, Gaby Böhme, Dr. chol. per. Ricardo “el popular” Chero, Stefanie Bröhl, Rubén Lara, Werner Ekau and all my former fellow students and professors who all have to bear parts of the blame that I completed this thesis. I also want to thank Daniel Lluch-Cota and the fisheries ecology gang of CIBNOR who in the end are responsible that my scientific interest took the direction that it did.

But after all, most important was Marlene during these last years and she most deserves my thanks...

**Thank you!**

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## Abstract

Marine organisms are influenced in their population dynamic and life history by environmental variability and fishery and cephalopods have been found to be especially plastic in their response to exogenous factors. However, underlying mechanisms of these interactions are often unclear and have been found to be complex. The ommastrephid jumbo squid (*Dosidicus gigas*) is an important component in the dynamic ecosystems of the Eastern Pacific Ocean and has gained considerable economic importance in the last two decades. Nearly simultaneously a range expansion to higher latitudes has been observed in both hemispheres. Like other cephalopods it is highly variable and rapidly changes abundances of its populations and their size structure. A hypothesis that proposes a complex population structure with three sub-groups related to reproduction is widely accepted. Its life history parameters published in the past often have not been concordant between different studies, areas and periods.

The present thesis had two main goals: (1) analyse data of the industrial jig fishery on *D. gigas* in the Peruvian exclusive economic zone to identify the biological response of *D. gigas* to environmental variability and fisheries, and (2) understand the mechanisms of this response. To realize this, traditional methods of the fishery science were used in a modified form to be able to apply them with temporally variable parameters to large data sets covering long periods.

Results show that the morphological and life history traits of *D. gigas* respond highly variable to changing environmental conditions and that fishery impacts indirectly and rather positive through the reduction of competitors and predators. A synchronous change in the state of expression of traits occurred after the strong La Niña/El Niño-sequence 1996 to 1998. The elevated energetic requirements of the new states compared to those before the shift lead to the conclusion that energy availability that in the Humboldt Current System is related to different water masses, is the governing factor for the observed change of life history traits. The changes in traits follow an energy optimization strategy

that allows jumbo squid to adjust to changing availability of prey and emphasize either in survival of the population or the increase of individual fitness. Temporal decoupling of maturation processes of the two sexes and the population energy storage strategy basing on cannibalism further optimize the use of energy and help to explain the extremely high assimilation efficiencies found for cephalopods in general in the past. Results are interpreted under the assumption of size-defined, discrete sub-populations and it is proposed that instead of the three discrete groups a change between two size-extremes exists related to the available energy.

Spatiality, although not directly addressed here, has resulted to be of importance and needs to be considered in future studies. Observed plasticity and the underlying energy optimization strategy are especially pronounced in jumbo squid but certainly not unique. The results of this thesis can help to identify similar schemes of adjustment of biological traits to exogenous factors in other marine species and consider them in their assessment and management to reach sustained fisheries under variable environmental conditions.

## Resumen

La dinámica poblacional y la historia de vida de los organismos marinos son influenciados por la variabilidad del ambiente y de la pesca y los cefalópodos son especialmente plásticos en su respuesta a los factores exógenos. Sin embargo, los mecanismos subyacentes de estas interacciones a menudo son poco claros y, en general, complejos. La pota (*Dosidicus gigas*), un calamar ommastreído, es un componente importante en los ecosistemas dinámicos del océano Pacífico Oriental ya que ha adquirido una considerable importancia económica en las últimas dos décadas. Casi simultáneamente se ha observado una ampliación del rango de distribución a latitudes más altas. Al igual que otros cefalópodos las abundancias y la estructura de tamaños de sus poblaciones son muy variables. Una hipótesis que propone una estructura poblacional compleja con tres subgrupos relacionado con la reproducción es generalmente aceptada. Sus parámetros de historia de vida publicados en el pasado muchas veces no han sido concordantes entre los diferentes estudios y periodos y las diferentes zonas.

La presente tesis tuvo dos objetivos: (1) analizar los datos de la pesquería industrial de *D. gigas* en la zona económica exclusiva del Perú para identificar los vínculos entre la variabilidad del medio ambiente, la pesca y la respuesta biológica de *D. gigas* y (2) entender los mecanismos subyacentes de esta respuesta. Para realizar esto, se usó los métodos de las ciencias pesqueras modificados para ser capaz de aplicarlos con parámetros temporalmente variables a datos largos que cubren largos periodos de tiempo.

Los resultados muestran que las características morfológicas y de la historia de vida de *D. gigas* responden de manera altamente variable a los cambios de las condiciones ambientales y que los impactos de la pesca durante el mismo periodo son indirectos y más bien positivos a través la reducción de competidores y depredadores. Un cambio sincrónico en el estado de expresión de las características de la historia de vida se produjo después de la fuerte secuencia de La Niña/El Niño de 1996 a 1998. Los requerimientos energéticos de los nuevos estados son elevados comparados con los de antes. Eso lleva a la conclusión

de que la disponibilidad de energía, que en el sistema de corrientes de Humboldt es relacionado a diferentes masas de agua, es el factor dominante para el cambio observado de las características de la historia de vida. Los cambios en las características ocurren según una estrategia de optimización de energía que permite que la pota pueda adaptarse a la disponibilidad variable de presa y destacar o en la supervivencia de la población o en el aumento de la fitness individual. El desacoplamiento de los procesos de maduración de los dos sexos y el almacenamiento poblacional de energía basados en el canibalismo optimizan el uso de la energía disponible en el ecosistema más y ayudan a explicar la altísima eficiencia de asimilación encontrada en cefalópodos generalmente. Los resultados se interpretan bajo el supuesto de que hay discretas subpoblaciones definidas por su tamaño, y se propone que en lugar de ellas existe un cambio gradual entre dos extremos de tamaño en relación a la disponibilidad de energía.

Espacialidad, aunque no tratada directamente aquí, ha resultado a ser de importancia y debe ser considerado en futuros estudios. La plasticidad observada y la estrategia de optimización de energía subyacente destacan especialmente en *Dosidicus gigas*, pero ciertamente no son únicos. Los resultados de esta tesis pueden ayudar a identificar esquemas similares en el ajuste de las características biológicas a factores exógenos de otras especies marinas y considerarlas en su evaluación y gestión para llegar a pesquerías sostenidas considerando las condiciones ambientales variables.

## Zusammenfassung

Marine Organismen sind generell durch Umweltvariabilität und wechselnde Fischerei in ihrer Populationsdynamik und *Life History* Charakteristika beeinflusst und Cephalopoden haben sich als besonders plastisch in ihrer Reaktion auf exogene Faktoren gezeigt. Allerdings sind zugrunde liegende Mechanismen oft unklar, und in der Regel komplex. Der ommastrephide Humboldtcalmar (*Dosidicus gigas*) ist ein wichtiger Bestandteil der dynamischen Ökosysteme des östlichen Pazifiks, der in den letzten zwei Jahrzehnten auch erheblich an wirtschaftlicher Bedeutung gewonnen hat. Fast gleichzeitig wurde in beiden Hemisphären eine Expansion seines Verbreitungsgebietes in höhere Breiten beobachtet. Wie andere Cephalopoden ist er äußerst variabel in Abundanz und Größenstruktur seiner Populationen und eine Hypothese, nach der eine komplexe, dreigeteilte Populationsstruktur mit Hinblick auf die Reproduktion besteht, ist allgemein anerkannt. In der Vergangenheit veröffentlichte Charakteristika der *Life History* aus verschiedenen Studien, Gebieten und Zeiträumen sind oft widersprüchlich.

Die vorliegende Dissertation hatte zwei Ziele: (1) die Analyse der Daten der industriellen Fischerei auf *D. gigas* in peruanischen Gewässern zur Identifikation seiner biologischen Antwort auf Umweltvariabilität und Fischerei und (2) das Verstehen der zu Grunde liegenden Mechanismen dieser Antwort. Dazu wurden die analytischen Methoden der Fischereiwissenschaft erweitert, um sie mit zeitlich variablen Parametern auf große Datenmengen anzuwenden, die lange Zeiträume abdecken.

Die Ergebnisse zeigen, dass die morphologischen Charakteristika und die Charakteristika der *Life History* von *D. gigas* sehr variabel auf veränderliche Umweltbedingungen reagieren und Auswirkungen der Fischerei indirekt und eher positiv sind durch die Reduktion von Konkurrenten und Predatoren. Eine synchrone Veränderung der Charakteristika fand nach der starken La Niña/El Niño-Sequenz von 1996 bis 1998 statt. Der erhöhte Energiebedarf der neuen Zustände führt zu der Annahme, dass die Nahrungsverfügbarkeit, die im Humboldtstromsystem an Wassermassen gekoppelt ist, der steuernde Faktor für die Aus-

prägung der Charakteristika ist. Die Änderungen der einzelnen Charakteristika der *Life History* folgen einer Strategie der Energieoptimierung, die dem Humboldtkalmar die Anpassung an wechselnde Verfügbarkeit von Beute erlaubt. Dabei wird entweder das Überleben der Population betont oder die Steigerung der individuellen Fitness. Die zeitliche Entkoppelung der Reifung der beiden Geschlechter sowie die Energiespeicherung in der Population an sich auf Basis von Kannibalismus optimieren die Nutzung der verfügbaren Energie weiter. Diese Strategien helfen, die beobachtete hohe Effizienz bei der Nahrungsassimilation von Cephalopoden im Allgemeinen zu erklären. Die Ergebnisse werden im Hinblick auf die bestehende Hypothese der großendefinierten, diskreten Subpopulationen interpretiert und es wird angenommen, dass statt drei diskreten Gruppen eine schrittweise Veränderung zwischen zwei Größenextremen wahrscheinlich ist, deren exakter Verlauf bestimmt wird von der Energieverfügbarkeit im Ökosystem.

Es hat sich gezeigt, dass räumliche Faktoren, obwohl hier methodisch nicht direkt angesprochen, eine wichtige Bedeutung haben und in künftigen Studien berücksichtigt werden müssen. Die hier beobachtete Plastizität und die zugrunde liegende Strategie der Energieoptimierung sind besonders ausgeprägt im Humboldtkalmar, aber mit Sicherheit nicht einzigartig. Die Ergebnisse dieser Arbeit können dazu beitragen, ähnliche Veränderung der Charakteristika der individuellen Entwicklungsgeschichte in anderen marinen Arten zu identifizieren und sie in der Bewertung und Management einzusetzen und nachhaltige Fischerei unter variablen Umweltbedingungen zu erreichen.

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## Abbreviations

AC	Arctic current
ACI	Arctic circulation index
ACP	Antarctic circumpolar current
BC	(peninsula) Baja California, Mexico
CC	California current
CCS	California current system
CCW	cold coastal waters
CENSOR	EU-project “Climate variability and El Niño Southern Oscillation: Implications for natural coastal resources and management”
CPUE	catch per unit of effort
CRD	Costa Rica dome
CV	climate variability
DMSp-OLS	Defense Meteorological Satellite Program-Operational Linescan System
EBCS	eastern boundary current system
EC	equatorial current
EEZ	exclusive economic zone
ELEFAN I	FAO expert system for length frequency analysis
EN	El Niño
ENSO	El Niño southern oscillation
EPO	Eastern Pacific ocean
ESS	evolutionarily stable strategy
ESW	equatorial surface waters
ETP	eastern tropical Pacific
EUC	equatorial undercurrent
EV	environmental variability
EwE	Ecopath with Ecosim
FAO	Food and Agriculture Organization of the United Nations
FiSAT II	fish stock assessment tool (version II) of FAO and ICLARM
GAM	generalized additive model
GCM	general circulation model
GoC	Gulf of California, Mexico
HC	Humboldt current
HCLME	Humboldt current large marine ecosystem

## ABBREVIATIONS

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HCS	Humboldt Current System
IBM	individual-based model
IMARPE	Instituto del Mar del Perú - Peruvian Institute of the Sea
IPCC	Intergovernmental Panel on Climate Change
IPO	interdecadal Pacific oscillation
kPa	Kilopascal, 1 kPa = 0.01 bar
LFA	length-frequency-analysis
LN	La Niña
MI	maturity index
ML	mantle length
ML <sub>50%</sub>	size of massive maturity
ML <sub>mean</sub>	size-at-(first)-maturity
MPA	modal progression analysis
MW	mixing waters
NAO	North Atlantic oscillation
NEC	north equatorial current
NECC	north equatorial counter current
Niño 1+2	the monitoring areas Niño 1 and Niño 2 combined (80°-90°W, 0°-10°S)
NPC	North Pacific current
OML	oxygen minimum layer
OMZ	oxygen minimum zone
PCC	Peru counter current
PDO	Pacific decadal oscillation
SAW	sub-Antarctic waters
SEC	south equatorial current
SENARPESCA	Servicio Nacional de Pesca (national fisheries service of Chile)
SM	structured model
SOI	southern oscillation index
SPC	South Pacific current
SPM	surplus production model
SRA	stock-recruitment analysis
SST	sea surface temperature
SSTA	sea surface temperature anomalies
SSW	subtropical surface waters
TSW	tropical surface waters
VBGF	von Bertalanffy growth function

## CHAPTER I: Overview

### 1 - Thesis outline

The present doctoral thesis investigates the influences of fishery and environmental factors on the ommastrephid cephalopod jumbo squid (*Dosidicus gigas*) in the northern part of the Humboldt Current System. It uses mainly data collected by numerous IMARPE technical onboard observers in the industrial fisheries of this species operating in the Peruvian EEZ in the period from 1990 to 2007. Methods used in this thesis comprise a number of methods of fishery biology amplified to consider dynamics of the species of interest under consideration of temporal and – in parts – spatial aspects. This doctoral project was associated with the EU-project CENSOR (Climate variability and El Niño Southern Oscillation: Implications for natural coastal resources and management, contract 511071).

The thesis is divided into four main sections: the introduction, the hypothesis, the investigative part and the synopsis and outlook. It is thematically finalized with a conclusion.

In CHAPTER II after an introduction on cephalopods and *D. gigas*, the Eastern Pacific Ocean, the distribution area of jumbo squid is outlined and the northern HCS, the actual study area in which this work focuses is presented in more detail. An additional part illuminates environmental variability (EV) and biological response and gives examples that go beyond pure empiricism and that are able to show underlying mechanisms that link EV and biology.

CHAPTER III consists of a published paper that develops the hypothesis on the triad migration-maturation-growth that tries to link several aspects of observed changes in ecology of *D. gigas* and gives a road map for the following work and the thesis. Here tempo-

ral and spatial aspects of the environmental variability and the biological response are identified.

The following CHAPTER IV comprises four studies (one published, one accepted and two submitted) that deal with the hypothesis developed in the previous chapter more detailed and analyses available data. The first part of this chapter temporally was the first study realized and describes first observations on biological traits of *D. gigas*. It tries to find an empirically connection to EV and a possible explanation for these observations. The following two parts analyse the data more thoroughly with respect to population structure. Of these, one manuscript is emphasizing on reproduction and the other on growth. The analysis in both studies use methods of the fishery biology. To cope with the tremendous amount of data that covers a period of nearly two decades and to be able to understand the preliminarily discovered changes in biological traits these methods had to be amplified. As an explanation for the great variability of traits, their habitat-dependency related to physical and biotic characteristics of watermasses is discussed. The final part of this chapter reviews the background of the high cannibalistic rate observed in many cephalopods and amplifies a hypothesis, the population energy strategy. It links cannibalism to environmental variability and allows *D. gigas* and other cephalopods to optimize the use of available energy.

CHAPTER V contains synopsis and outlook. The synopsis integrates the results of the former parts with the “energy optimization strategy” that emphasizes on the temporal variability of the observed phenomena in relation to environmental variability. At present the synopsis is a manuscript in preparation for submission. Results, however, indicate the importance of spatial factors. The second part of this chapter, the outlook, contains a published review that lists ecological models assumed to be applicable in future studies and projects under this focus. Several types of models that are able to integrate environmental variability and fishery-related factors are presented and analysed with respect to spatiality, data and skill requirement as well as general strengths and weaknesses. Potential pitfalls related to spatiality and complexity of quantitative methods and more generally the linkage of environmental variability to biological entities are analysed.

CHAPTER VI very shortly concludes the main findings of the dissertation. To prevent double entries CHAPTER VII lists the collected references of all chapters alphabetically.

## 2 - Contributions to the manuscripts

### Manuscript 1:

**Keyl F**, Argüelles J, Mariátegui L, Tafur R, Wolff M, Yamashiro C (2008) A Hypothesis on Range Expansion and Spatio-Temporal Shifts in Size-at-Maturity of Jumbo Squid (*Dosidicus gigas*) in the Eastern Pacific Ocean. CalCOFI Rep 49:119-128

The idea of the triad hypothesis and the concept of the publication were done by me. The manuscript was elaborated by me. All other authors contributed with ideas. All figures were conceptualized and realized by me.

### Manuscript 2:

Argüelles J, Tafur R, Taipe A, Villegas P, **Keyl F**, Dominguez N, Salazar M (2008) Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989–2004. Prog Oceanogr 79:308-312

Basic idea and elaboration of the publication was done by JA, I contributed with the idea of the connection to environmental variability and provided possible timeseries of environmental variability. I supplied parts of the discussion and introduction.

### Manuscript 3:

Tafur R, **Keyl F**, Argüelles J (subm) Reproductive biology of the jumbo squid (*Dosidicus gigas*) in relation to environmental variability of the northern Humboldt Current System. Mar Ecol Prog Ser

Ideas, concept and elaboration of the publication were done by me. All analyses were conceptualized and conducted by me. RT & JA contributed with ideas to the manuscript,

JA and RT provided data, databases were elaborated together. All figures were conceptualized and realized by me.

#### **Manuscript 4:**

**Keyl F**, Argüelles J, Tafur R (subm) Inter-annual variability of population structure, age and growth of jumbo squid (*Dosidicus gigas*) in the Humboldt Current System. Mar Ecol Prog Ser

Ideas, concept and elaboration of the publication were done by me. All analysis were conceptualized and conducted by me. The Matlab script for the decomposition of the length frequencies was written by me. JA contributed with ideas to the manuscript, JA and RT provided data, databases were elaborated together. All figures were conceptualized and realized by me.

#### **Manuscript 5:**

Ibáñez C, **Keyl F** (in press) Cannibalism in Cephalopods. Rev Fish Biol Fish

Idea and concept by CI, I contributed with ideas, especially those related to energy and the population energy storage. The manuscript was elaborated together. Figures were realized together.

#### **Manuscript 6:**

**Keyl F**, Yamashiro C, Ibáñez C, Argüelles J, Tafur R, Wolff M (in prep) A strategy of trait optimization as response to environmental variability: the case of the jumbo squid.

Ideas, hypotheses and concept of the manuscript were done by me. All other authors contributed with ideas to the manuscript and brought me back down to earth when necessary. Elaboration of the manuscript was done by me together with CI and MW. Additional data that was not taken from other MS were provided from JA, RT and CY. All figures were conceptualized and realized by me.

**Manuscript 7:**

**Keyl F, Wolff M (2008) Environmental Variability and Fisheries: What Can Models Do?**  
Rev Fish Biol Fish 18:273-299

Basic idea for the review was by MW. Conceptualization as well as search for and selection of the models were done by me. Evaluation of the models was done by me with assistance from MW. The discussion part was conceptualized and elaborated by me. MW contributed in the elaboration of the manuscript. All figures were conceptualized and realized by me.

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## CHAPTER II: Introduction

### 1 - General characterization of cephalopods

#### 1.1 - Systematic and anatomy

The group cephalopod contains all nautilus, squids, cuttlefish and octopi and is part of the molluscs. Cephalopods are known since the early Cambrian, roughly 500 Mio years ago (Westheide & Rieger 1996). The group is divided into three subclasses: (1) *Coleoidea* that contains most recent genus and species (2) *Nautiloidea* with the sole recent genus *Nautilus* that contains 5 recent species which is also the only cephalopod group that has not reduced the original external shell and (3) *Ammonoidea* that became extinct some 65 Mio. years ago in the upper Cretaceous (Roper 1984). The known 650 (Boyle 1983) to 1000 (Roper et al. 1984) recent species are organized into 43 families. The coleoid cephalopods comprise the recent decapods *Sepioidea*, *Teuthoidea* and *Vampyromorpha* as well as the fossil *Belemnoidea*; the octopods consist of *Cirrata* and *Incirrata*.

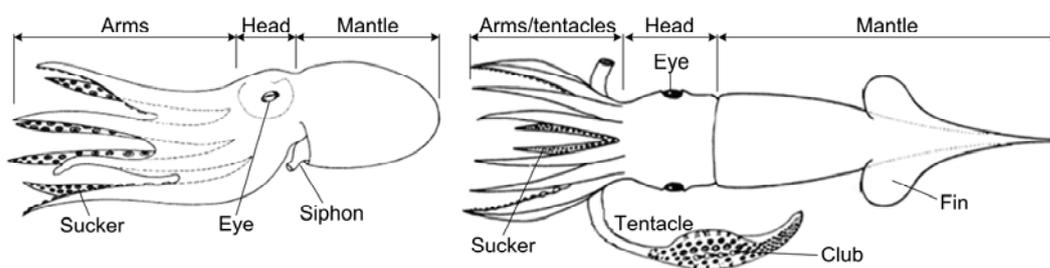
Cephalopods are uniquely marine and found to depths of 5500 m and possibly deeper. Pelagic species are good swimmers and show daily vertical and geographical seasonal migratory behaviour but many species are also benthic (Mangold 1987). Some species appear to be cosmopolitans. Some larger pelagic species – mainly the oceanic squids of the oegopsid family Ommastrephidae, the flying squids – can reach swimming speeds of 2 m/s in the water and manage to leave the water and “fly” with up to 7 m/s or more. The species of interest of the present work, *Dosidicus gigas*, belongs to this family.

Main characteristics of cephalopods are (1) the name-giving *cephalopodium*, a head-arm-complex that is used for predation and in case of many octopods for locomotion, (2) the siphon, thought to have evolved from the molluscan foot, (3) a strong chitinous, beak-like

jaw that allows them to bite their food to bits, (4) relatively large image forming eyes and (5) a shell that identifies them as conchiferan molluscs, although the shell is usually internal or secondarily reduced (Roper et al. 1984, Westheide & Rieger 1996, Young et al. 2008).

Sizes of cephalopods range from about 15 mm to 20 m with a maximal weight of over one ton (Boyle 1983). The average size of commercial species is 20 to 30 cm total length and 0.1 to 1 kg and their total muscle tissue comprises 75% to 90% of a cephalopod's live weight (Semmens et al. 2004).

Their body with mantle, head, arms and tentacles is three-partite (Figure II-1). The mantle is a muscular cylinder that contains most organs and a water-filled cavity. Mantle contractions press water through the flexible siphon and pressure reaches 50 kPa and enables them to move and navigate backwards by jet-propulsion. Octopodid cephalopods have eight arms, the decapodids have two additional tentacles and nautiloidean cephalopods can have up to 90 arms. The arms are grouped in one or two rings around the mouth and are often highly differentiated with 1, 2 or 4 rows of suckers and different functions (Westheide & Rieger 1996). Usually one arm of the males is formed as *hectocotylus* that transmits spermatophores into the female's mantle cavity during mating. Before mating the spermatophores are stored in the Needham's sac from where they are passed to the female through a special duct of the *hectocotylus* if present (Boyle 1990).



**Figure II-1 A) Scheme of an octopodid cephalopod; B) Dorsal view of schematized decapodid cephalopod; siphon on the ventral side not visible; after Roper et al. 1984**

The buccal mass contains a freely movable and strong chitinous and beak-like jaw. It allows the cephalopods to dismember their food and together with arms and tentacles gives access to a large range of prey. Their tongue-like radula is used to transport food to the oesophagus (Westheide & Rieger 1996).

Cephalopods show a tendency to cerebralisation and are thought to be the most intelligent invertebrates (Dewar & Psych 2004) that may even have primary consciousness (Mather 2008). Sense organs are highly developed and especially the eyes are important. If cephalopods can see colours is not resolved for all species but nearly all studies discard colour vision. Chromatophore organs in their skin allow them to camouflage and bioluminescent light organs are used in communication. They have photoreceptors distributed over the body surface, statocysts in the head and mechano- and chemo-sensors in the skin. Experiments with *Octopus* showed that they can not hear but are able to perceive the vibrations of low-frequent oscillations (Boyle & Rodhouse 2005, Young et al. 2008)

In case of danger many cephalopods can expulse a secretion with melanin, the ink, to facilitate escape. In some species it also contains a toxic that paralyses the attacker or blocks its senses (Westheide & Rieger 1996, Boyle & Rodhouse 2005).

All species are dioecious and often but not always show clear sexual dimorphism in size, body proportions and the hectocotylus of the male as well as in behaviour (Boyle & Rodhouse 2005).

## **1.2 - Life history traits of cephalopods**

Exogenous factors have often been described to have an important influence on all life stages of cephalopods and it is assumed that cephalopods generally show plasticity in their life history traits as response to environmental variability (e.g. Boyle & Rodhouse 2005). Growth and reproduction related parameters are controlled by temperature, feeding level and light among other variables. The underlying relationships are not necessarily linear and seem to have thresholds as well as interactions with other controlling factors. Exogenous control of life history of cephalopods thus could be more complex than often proposed (Mangold 1987).

Generation times show interannual differences according to environmental conditions at least for some species of *Sepia* and *Loligo* (Boyle & Boletzky 1996). Mature males of many species, among these the ommastrephid species, are known to mate with immature females that, depending on the species, have differently formed external and internal spermatophore storing sites (Mangold 1987). This leads to delayed spawning, the fertilization of egg batches of females by various males and necessarily to a filial generation

with higher genotype diversity. The result is a higher adaptation capacity to changing environmental conditions and, through higher survival rates of at least parts of the progeny, higher individual fitness (Boyle & Rodhouse 2005).

Most recent coleoid cephalopods show monocyclic reproduction, i.e. they die after their first reproductive season. They often are relatively short lived and die after a phase of senescence that starts after reproduction and is the last phase in cephalopod life (Rodhouse 1998, Rocha et al 2001). It becomes noticeable by loss of appetite and lack of feeding with massive weight loss, skin retraction around the eyes, uncoordinated activity and white lesions on the skin that do not heal. Senescence finally leads to death and apparently all coleoid species and specimens are affected (Anderson et al. 2002). It is important to understand that the monocyclic reproduction couples size-at-first-maturity to terminal size.

As it is the case with short-lived fish and shrimps, recruitment of cephalopods often seems to consist of two unequal annual pulses (Pauly 1985). It is assumed that stock-recruitment relationships are even weaker than those of teleost fish with influencing factors of individual growth and survival highly connected to abiotic and biotic environment. However, these factors might be difficult to detect (Boyle & Boletzky 1996). As adults usually die after reproduction, population success depends on the survival of the offspring and reproduction strategies to secure survival of progeny vary in different species. They include floating eggs, benthic spawning, brood care, protective egg covers, large yolk and short incubation time of eggs among others (Amaratunga 1987). Egg number of sepioids and octopods is rather small and contrasting that of the pelagic ommastrephids (Boyle 1990) where a single large female can spawn up to 50 million eggs in several batches (*Dosidicus gigas*, Nigmatullin & Markaida 2008). The egg number is highly variable and in most cases related to size of the female (Mangold 1987). Egg size ranges from 0.8 mm to 1.7 cm (Roper et al. 1994) and hatching occurs after 2 days to several weeks (Boucher-Rodoni et al. 1987). The succession of larval stages that is generally found in molluscs is given up in the cephalopoda in favour of a paralarva that connects egg stage and adult life. The paralarva already has many features of the later adult and is considered a “mini-adult” (Boyle & Rodhouse 2005).

Very high conversion efficiency results in fast growth (Boyle & Boletzky 1996) that shows high variability on the species and individual level (Forsythe & Van Heukelem 1987). It is reported to slow down or even to stop completely after the onset of maturation (Boyle 1990). Among others, the von Bertalanffy growth function (VBGF), linear, asymptotic or exponential functions as well as combined functions with a seasonal component and multiphase models have been employed to describe cephalopod growth (e.g. Pauly 1985, Forsythe & Van Heukelem 1987, Wells & Clarke 1996, Lipinski 2002). Growth efficiency reaches values as high as 40 to 60% for the sedentary species (octopus and cuttlefish) and is assumed to be still 20 to 30% for the highly active oceanic squids (e.g. Nixon 1987, Boyle & Boletzky 1996).

Maturity of many pelagic and neritic species is related to migration patterns, currents, temperature and food supply (Boyle 1990). Spawning and maturation is affected by light, temperature and alimentation history. Seasonal spawning of a population thus would be the effect of a history of common environmental conditions of the individuals of a population sub-group (Mangold 1987). Temperature has a strong effect on growth rates and onset of maturity (Van Heukelem 1976, Mangold 1987) but has little consequence for fecundity itself (Richard 1970 in: Mangold 1987). In controlled experiments low food availability in late adult (maturing) phase has been found to produce accelerated maturing at smaller sizes while *ad libitum* feeding delays reproduction and allows individuals to grow larger. Starving in early stages in contrast leads to the opposite result: delayed maturation and a prolonged life span (Mangold 1987). Passing through the different life stages in case of the cephalopods may therefore be understood as exogenously determined (Anderson et al. 2002). Examples for this were given in Boyle & Rodhouse (2005): day-length for *Sepia* (Richard 1967), temperature for octopods and *Sepiotheutis* (various sources) and nutrition for *Eledone* (Boyle & Knobloch 1984). However, the multifactorial control of maturation is emphasized (Boyle & Rodhouse 2005).

### 1.3 - Trophic role of cephalopods

Cephalopoda are carnivore macrophages that opportunistically exploit the most abundant organisms at any time in their prey size range (Boyle 1990). They are able to hunt down fast moving prey such as fish, crustacean or smaller cephalopods and especially the larger specimens in a population are often cannibalistic (Boucher-Rodoni et al. 1987, Rodhouse & Nigmatullin 1996, Boyle & Rodhouse 2005). High protein quality of their food, very

high food conversion rates and short life spans translate to a lifetime food requirement that is as low as 2.5...3 times the final body mass for octopus and some 4...8 times for the more active squids which makes cephalopods interesting for aquaculture (O'Dor & Wells 1987, Wells & Clarke 1996, Boyle & Boletzky 1996). Interestingly, cephalopods only have restricted ability to store energy individually (O'Dor & Wells 1978, Molt-schaniwskyj & Semmens 2000). The pronounced digestive glands and muscle tissue in octopods have been proposed as storage organs (O'Dor & Wells 1978).

Cephalopods themselves are prey for toothed whales, seals, pelagic birds, and large fishes like e.g. tunas, billfishes, sharks and rays (Roper et al. 1984). Due to the large biomasses of their populations, some pelagic species are of great importance for apex predators (Clarke 1996a, b, c) and this importance suggests that cephalopods are an important link in the food web that is connecting lower and higher trophic levels. For 1972 it was estimated that sperm whales alone fed 100 Mio tons of squids (Clarke 1977 in: Nixon 1987) and it is assumed that some 34 Mio tons of squid is eaten annually by mammal and avian predators only in the Antarctic (Clarke 1987).

Following heavy fishing on teleost resources it has been observed that cephalopod populations increased in size due to the reduction in food competitors and predators. This may lead to high pressure on young fish by the cephalopod predation and a changed system with abundant cephalopod but reduced fish populations (Boyle & Boletzky 1996).

## 2 - The jumbo squid *Dosidicus gigas*

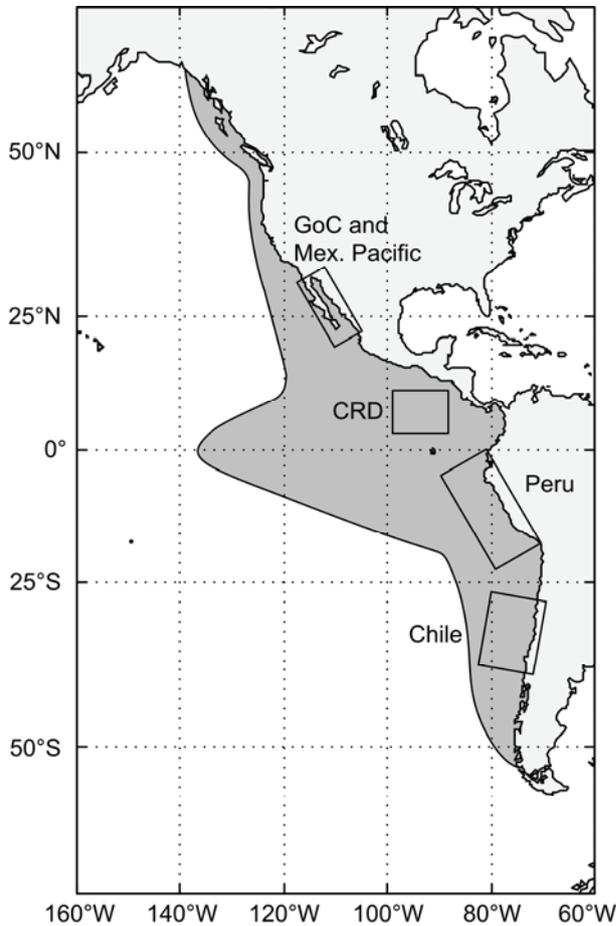
### 2.1 - Description and distribution

The jumbo squid belongs to the oegopsid family Ommastrephidae, the “flying squids” whose 23 members are found in all oceans with the exception of the Polar Regions (Roper et al. 1984, Gilly et al. 2006). *Dosidicus gigas* itself is endemic to the Eastern Pacific Ocean (EPO) and was generally found between 40°N and 45°S in southern Chile (Figure II-2). Around the equator its distribution area has a westward extension to 135°W. Highest abundances are found between Baja California and Northern Chile (Nigmatullin et al. 2001) and up to 200 to 250 nm from the coast (Nesis 1983, Erhardt et al. 1983). In the last 10 years a range expansion to higher latitudes has been observed and specimens have been caught off Alaska and southern Chile (Gilly et al. 2006, Zeidberg & Robison 2007, Field et al. 2007). In the Eastern Pacific it is the most abundant squid and an important element of the ecosystems (Anderson & Rodhouse 2001).

A number of synonymous common names for jumbo squid exist in both English and Spanish. A second English name is Humboldt squid and both English common names frequently are varied as jumbo flying squid and Humboldt flying squid taking into account the numerous stories that report leaps out of the water in pursuit of flying fish. In Mexico it is officially named *calamar gigante* –gigantic squid – but due to its colour and its murderous fame it is also nicknamed as *diablo rojo* – red devil. In Peru it is called *pota* and in Chile *jibia*.

*D. gigas* is a large squid with a large and thick walled, muscular mantle with rhomboidal fins (Figure II-3). Arms and the distal ends of the tentacles are closely covered with 100 to 200 suckers that contain toothed chitinous rings to prevent sliding (Roper et al. 1984). It shows sexual dimorphism in several external features. The mantle of the females is more barrel-like widened in the centre and tangibly thinner and they tend to have stronger

beaks. Males in average and maximum size are smaller and have their fourth left or right arm hectocotylized. (Nesis 1983).

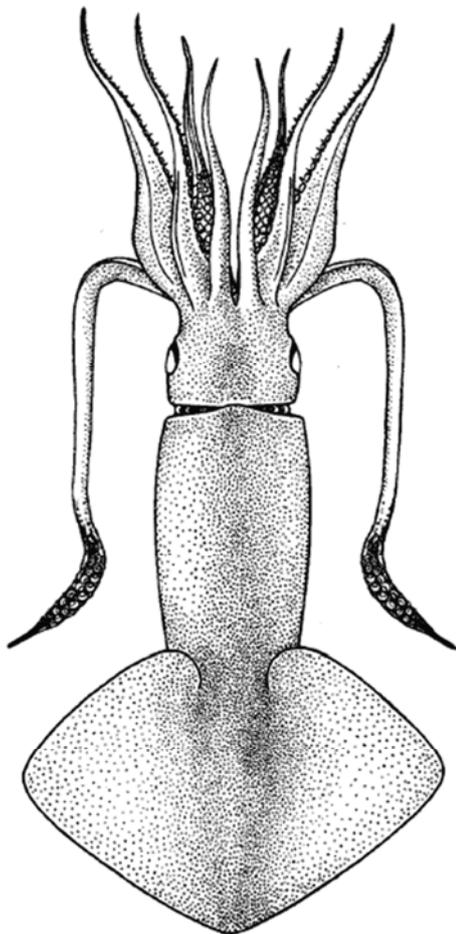


*Figure II-2: distribution range of D. gigas (dark grey) after Gershanovich et al. (1974), Roper (1984), Hochberg & Hatfield (2006) and Cubillos & Ibáñez (2007); rectangles: main fishing areas; GoC: Gulf of California; CRD: Costa Rica Dome*

*Dosidicus gigas* is a nerito-pelagic squid found from the surface to a depth of 1200 m (Nigmatullin et al. 2001) but it can also occur in nearshore waters (Roper et al. 1984). Usually it is found in waters with temperatures of 15 to 28°C but it tolerates temperatures from 4 to 32°C (Nigmatullin et al. 2001). The distribution area of jumbo squid coincides with the 0.8 mg/m<sup>2</sup>-phosphate isoline in the upper layer which is assumed to be equal to the limit of highly productive waters (Aleksandronets et al. 1983 in Nigmatullin et al. 2001). High densities of *D. gigas* are generally found in areas of high primary production (Nigmatullin et al. 2001). More recent studies hypothesize that the distribution area of jumbo squid may be defined by the extension of the oxygen minimum zone (OMZ) as it is not only able to tolerate hypoxic conditions but also actively hunts there (Gilly et al 2006, Rosa & Seibel 2008). The observed expansion of the OMZ in the world oceans in

the last years (Stramma et al. 2008) is seen as a possible reason for the intrusion of *D. gigas* into new areas north and south of its former distribution range (Gilly et al. 2006).

Adult specimens undertake diurnal vertical migrations into and even below the oxygen minimum layer (Nigmatullin et al. 2001, Gilly et al. 2006). Horizontal migrations are interpreted as seasonal feeding migrations (Nesis 1983, Ehrhardt et al 1983) certainly on the basis of similar migrations that have been found for other ommastrephid squids (e.g. *Illex argentinus*: Waluda et al. 2001, 2008, *Ommastrephes bartramii*: Ichii et al. 2009).



*Figure II-3: dorsal view of D. gigas; taken from Roper (1984)*

Seasonal migrations occur in large schools of thousands of animals that possibly move between coastal waters and between spawning areas (above the continental slope) and alimentionation areas (further offshore) with swimming speeds of up to 25 km/h (Nesis 1970, Nigmatullin et al. 2001). However, these schemes have not been verified and until now no migration scheme has been published for *D.gigas* of the southern hemisphere.

## 2.2 - Diet and feeding

Total abundance of *D. gigas* was estimated to be 7 to 10 million tons and based on a daily food intake of 7% of body weight it is thought that they consume as much as 200 to 250 million tons per year (Bazanov 1987 in Nigmatullin et al. 2001). However, these values contradict the generally assumed conversion efficiency of squids of 20% and more (Nixon 1987, Boyle & Boletzky 1996). During its rapid ontogenesis it is feeding from level II to level IV in the food web, where it is an important component of passing on energy from lower levels to the apex predators (Nigmatullin et al. 2001). *D. gigas* is considered a key species within its trophic system (Ruiz-Cooley et al. 2006, Field et al. 2007, Rosas-Luis et al. 2008, Taylor et al. 2008).

Stomach content analyses revealed a high number of species of fish, molluscs and crustacean that varied temporally and spatially in importance (Markaida & Sosa-Nishizaki 2003, Markaida 2006, Ibáñez et al. 2008). Most important prey items are the mesopelagic myctophids and euphausiid crustaceans (Nesis 1983, Markaida & Sosa-Nishizaki 2003, Tam et al. 2008, Taylor et al. 2008) that can rapidly build up huge biomasses (Froese & Pauly 2007). Jumbo squid is considered a generalist (Ibáñez et al. 2008) that feeds on all moving prey if it is abundant and of the appropriate size (Nesis 1970, 1983, Markaida & Sosa-Nishizaki 2003); a behaviour similar to that of most other cephalopods. This generalist feeding behaviour makes schooling species especially suitable prey for *D. gigas* (Markaida & Sosa-Nishizaki 2003). Size range of prey, the “predation window” (Claessen et al. 2000, 2002) is between 5% and 87% of its own mantle length (Nigmatullin et al. 2001, Markaida & Sosa-Nishizaki 2003).

The high percentage of empty stomachs, found even in areas with high prey abundance, suggest rapid digestion (Erhardt et al. 1983). Main feeding times were thought to be after sunset and before sunrise near the surface and illuminated prey will be rapidly attacked. This fact is used in the jig fishing method, where strong floodlights are used (Nesis, 1983). Other investigators described surface feeding during day and night (Nixon 1987) and feeding in deeper waters (Zeidberg & Robison 2007) where *D. gigas* is seeking shelter in the OMZ during the day (Gilly et al. 2006). Especially juvenile and subadults hunt in schools but generally similar-sized individuals hunt in small groups (Nigmatullin et al. 2001, F. Keyl, ZMT, personal observations).

Cannibalism in jumbo squid is marked and regularly high percentages of conspecifics are found in the stomachs especially of larger specimens (Markaida & Sosa-Nishizaki 2003, Markaida 2006, Ibáñez et al. 2008). High cannibalistic rates (up to 75% of weight, IMARPE, unpublished data) at least in parts are supposed to be an artefact of fisheries due to two reasons: (1) fisheries are usually size-specific, taking individuals with a mantle length (ML) of more than 200 mm, i.e. the larger, more cannibalistic specimens are disproportionately represented in many stomach analyses and (2) jumbo squid as target species of the fisheries is abundant during the fishing operations and therefore can become main target for its conspecifics. Cannibalistic items are very present in the stomachs and a weight fraction of 5 to 30% has been reported often, highlighting the importance of cannibalism in the diet of *D. gigas* (Markaida 2006, Ibáñez et al. 2008). Although not yet proven by published stomach content analyses, it has been supposed that females could be more cannibalistic than males (Clarke & Paliza 2002, F. Keyl, ZMT, personal communication). Cannibalism generally may allow schooling cephalopods to migrate through “deserted” regions, e.g. for rapid dislocation to spawning grounds (O’Dor & Wells 1987) but this has never directly been shown in case of *D. gigas*.

*D. gigas* is important as dietary component of its predators. Already as juvenile it is one of the principal prey species of sharks (Aguilar-Castro & Galván-Magaña 2003) and big pelagic fish (Abitia-Cárdenas *et al.* 1999, 2002, Rosas-Aloya *et al.* 2002). Adults are the main food of sperm whale (Ruiz-Cooley *et al.* 2006), swordfish, shark, a number of whales and other marine mammals (Roper *et al.* 1984, Markaida & Sosa-Nishizaki 2003, Rosas-Luis *et al.* 2008, Tam *et al.* 2008, Taylor *et al.* 2008).

### **2.3 - Growth and reproduction**

Maximum size, growth rates and longevity of *D. gigas* found in past studies (Nesis 1970, Ehrhardt *et al.* 1983, Arkhipkin & Murzov 1986, Argüelles 1996, Argüelles *et al.* 2001, Markaida *et al.* 2004, Nevárez-Martínez *et al.* 2006) are not consistent. While for growth rates values between 200 to 995 mm/yr have been found, longevity is reported to lie between 1 and 4 years. The biggest individuals caught off Chile waters supposedly measured 4 m with a mantle length (ML) of 1500 mm. Most animals are between 500 to 800 mm ML and a weight of 2 to 3 kg (Roper *et al.* 1984) although this weight seems to low. The biggest specimens reported from Peru reach 1250 mm ML and weighed more than 60 kg (R. Tafur, IMARPE, personal communication). Fastest growing specimens off South

America are thought to be the winter-hatched (August to September), while the summer/autumn (February to May) hatched specimens are slowest growing (Nigmatullin et al. 2001).

Size-at-maturity and age-at-maturity differ between sexes. As *D. gigas* is monocyclic and dies after its first reproduction season, size-at-first-maturity is equal to size-at-maturity. To simplify matters in the present work the term “size-at-maturity” will be used exclusively. It is also noteworthy that consequently size-at-maturity is related to maximal size. Males can reach maturity with a length of 180 to 250 mm ML (corresponding to ages of 2 to 3 month) and females with 350 to 400 mm ML at ages from 4 to 6 month (Roper et al. 1984). However, it is widely accepted that the population structure of *D. gigas* is more complex and consists of three distinct groups of size-at-maturity: a group of small-sized specimens occurring mainly in the equatorial region (males mature with 130...260 mm ML, females with 140...340 mm), a group of medium-sized specimens found throughout the distribution area (240...420 mm and 260...600 mm respectively) and a third group restricted to the southern and northern distribution limits comprising specimens that reach maturity at ML of 400...500 mm and 550...650 mm respectively and more (Nesis 1970, 1983). Data that support this assumed distinction is limited and the separation of larger specimens into two groups has already been doubted by the author himself in the first publication on the topic (Nesis 1970). Although doubtful, the fundamental review of Nigmatullin et al (2001) on *D. gigas* has republished this population structure and following publications have taken it for granted. Possible explanations given for these size groups were phenotypic plasticity that responds to temperature or genetically distinct sub-groups (Nesis 1970, 1983).

Population structure of jumbo squid seem to vary drastically between the years (Markaida 2006, Bazzino et al. 2007) and a cohort analysis found up to five cohorts per year with different hatching times in Mexican waters (Ehrhardt et al 1983). As in case of other ommastrephid squids, the female:male-ratio of *D. gigas* has been found to be in favour of the females. But again, the exact values vary greatly between study areas and years fluctuating between 1:1 and 24:1 (e.g. Nesis 1983, Markaida & Soshi-Nishizaki 2001, Tafur et al. 2001, Ye & Chen 2007, Bazzino et al. 2007, Ibáñez & Cubillos 2007).

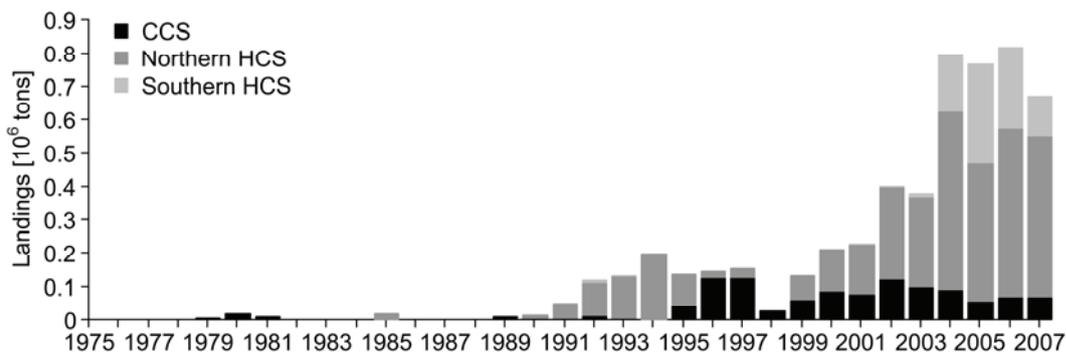
Overall reproduction pattern of *D. gigas* is monocyclic, as that of most cephalopods (Rocha et al. 2001). Male spermatophores in size are proportional to the individual's size while mature eggs always have a diameter of around or under 1 mm (Nesis 1983). *D. gigas* is a batch spawner (Rocha et al. 2001, Staaf et al. 2008, Nigmatullin & Markaida 2008) that can reach an overall potential fecundity of 32 Mio eggs per female and even more. This number by far represents the highest fecundity found among cephalopods and is related directly to female size. A female is thought to spawn 10 to 14 batches (Nigmatullin & Markaida 2008) and total egg mass is the largest of any squid.

Although only in the Gulf of California (GoC) egg batches of jumbo squids have been found in the wild (Staaf et al. 2008) other areas in which spawning is assumed to take place have been identified indirectly on the basis of observation of mating, occurrence of mature females and the presence of paralarvae. Such areas are central and northern Peruvian waters (Tafur et al. 2001), the Costa Rica Dome (CRD, Vecchione 1999, Ichii et al. 2002) and the GoC (Gilly et al. 2006). Although a considerable amount of mature females and males have been found in 2002 and 2003 in the Chilean Region IV (34°S to 40°S) neither paralarvae, spawned specimens (stage IV) nor actual spawning have been observed until present (Ibáñez & Cubillos 2007). Hatching of paralarvae in experiments occurred after an incubation time of the eggs of 3 to 4 days at temperatures of 28°C and 24°C (Ichii et al. 2002 and Staaf et al. 2008 respectively) and after 7 to 9 days at 18°C (Yatsu et al. 1999). In the latter study eggs kept at 22°C did not hatch.

## **2.4 - Fisheries and socio-economic importance of *D. gigas***

*D. gigas* is an important resource for directed and undirected fisheries in the GoC (Ehrhardt et al. 1983, Morales-Bojorquez et al. 2001), in the region of the CRD (Ichii et al. 2002) and off Peru and Chile (Taibe et al. 2001, see Figure II-4). Considering the landings, the fishery on *D. gigas* in 2006 grew to be the 12<sup>th</sup> largest in the world (FAO, <ftp://ftp.fao.org/FI/STAT/summary/a1e.pdf>). Highest catches were made in the pelagic fisheries off Peru by the combined efforts of an international industrial fishery and national artisanal fleets (Figure II-4). Especially in the central GoC and in northern and southern Peru artisanal jumbo squid fisheries create income for a large number of indirectly dependent inhabitants and are of great socio-economic importance (Badjeck 2008, IMARPE, unpublished data).

Landings, abundances (Yamashiro 1998, Rocha & Vega 2003, FAO FIGIS 2005, Markaida 2006, IMARPE unpublished data) and size compositions of the landings (Yamashiro 1998, Markaida et al. 2004, Díaz-Uribe *et al.* 2006) have been highly variable. Changes were especially marked during the strong El Niño (EN) 1997/98 in the Mexican and the Peruvian fisheries (Lluch-Cota et al. 1999, Morales-Bojórquez et al. 2001, Taípe et al. 2001, Nevárez-Martínez et al. 2001, Markaida 2006b, Yamashiro et al. 2007). In the area of the CRD high fishery yields were associated with the EN of 97/98 (fall 1997) and low ones with LN of fall 1999 (Ichii et al. 2002). The fishery in Chile until the end of the 1990s was nearly non-existent but after 2000 exploded in a few years to its maximum of nearly 300,000 t in 2005 (SENARPESCA, <http://www.sernapesca.cl/>).



**Figure II-4: landings of *D. gigas* in the Eastern Pacific Ocean.**

It is not clear why jumbo squid appears and disappears in certain areas as it did in the last decades (Klett 1996, Rubio & Salazar 1992, Markaida 2006, Yamashiro et al 2007, SENARPESCA). In warm years or warm periods in Peru a lower number of large-sized squid was found but instead small- and medium-sized specimen that dwelled closer to the coast. It was assumed that this is due to changes in the current patterns and the subsequent restructuring of the ecosystems (Nigmatullin et al. 2001). Abundance data of juvenile and adults of different cephalopod species have been connected to the Southern Oscillation Index (SOI) and the Trans Polar Index (TPI) that influence the mix layer zone via wind stress variability and subsequently the prey abundance of an area (Waluda et al. 2004). Abundance and catches of *D. gigas* in Peruvian waters and the northern HCS in general were related to SST and EN but these relations are only clear for the EN-period (Waluda et al. 2006) and do not hold when applied for the complete study period. However, Yamashiro et al. (1998) also mentioned a relation between stock parameters and water masses in the northern HCS. Mark-recapture experiments in Mexico have shown a sea-

sonal migration of *D. gigas* between the two coasts of the Gulf of California that define the local fishing seasons (Markaida *et al.* 2005).

With the exception of the off-shore fisheries in Chile, where it is taken as a bycatch in other fisheries, the fishery on jumbo squid is realized at night with the so-called squid jigs from specialized jigger boats under the employment of strong flood lights (Roper *et al.* 1984, Waluda *et al.* 2004). The industrial fishery is using automated jigging machines (Ichii *et al.* 2002).

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## 3 - Study area

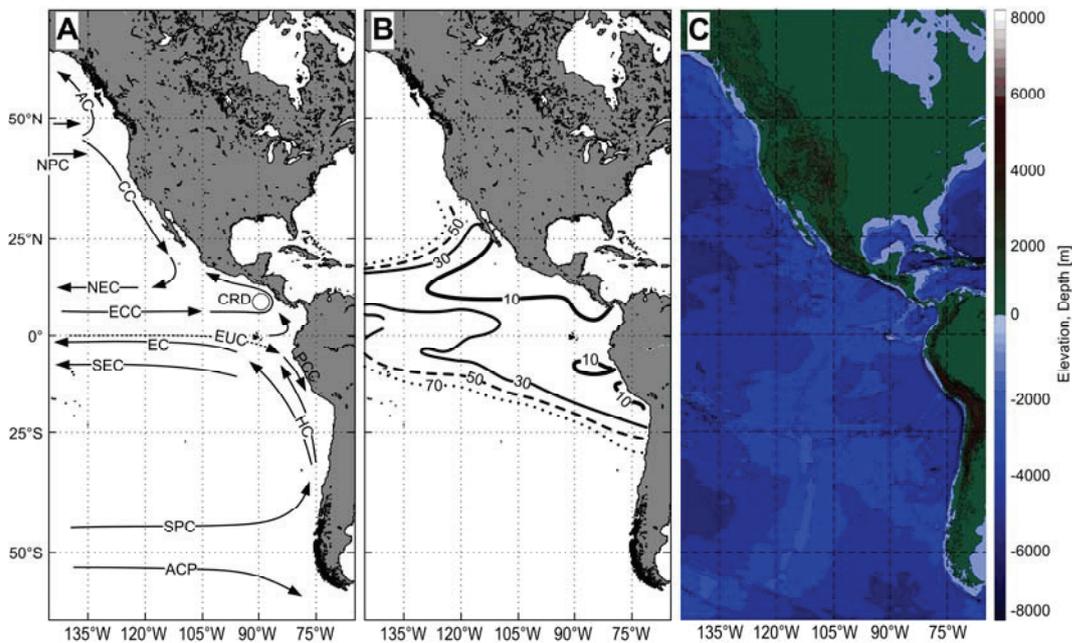
### 3.1 - The Eastern Pacific Ocean (EPO)

The region comprises two eastern boundary current systems, the Humboldt Current System (HCS) and the Californian Current System (CCS). The Eastern Tropical Ocean (ETO), a neurlgic region for world climate (Wang & Fiedler 2006, Kessler 2006) separates the two systems with its three westward equatorial currents: the south equatorial current (SEC, at 10°S), the equatorial current (EC) and the north equatorial current (NEC, at 10°N, see Figure II-5A). In a recent review the EC and SEC are seen as one current (Kessler 2006). Moreover, in the area the equatorial counter current (ECC) flows eastward at 5°N. The equatorial undercurrent (EUC) is a subsurface counter current steadily moving closer to surface during its eastward trajectory and establishing the Peru counter current (PCC), a southward flowing coastal surface current off the South American continent (Kessler 2006). This current is important for the oceanographic conditions of the northern HCS and known to have great influence on the ecosystems in this area (e.g. Morón 2000, Arancibia et al. 2007, Graco et al. 2007, Guevarra-Carrasco & Lleonart 2008).

Both systems, the HCS and the CCS are forming the eastern part of their respective Pacific gyres and are characterized by mesoscale eddies, meanders and extensive upwelling areas that are known to break down or intensify during El Niño and La Niña conditions respectively (Schmitz 1996, Morón & Sarmiento 1999, Anderson & Rodhouse 2001, Tomczak & Godfrey 2005 and see below). In both systems subsurface counter currents exist. While the CCS flows southward and merges with the NEC; the HCS on the contrary flows northward from the southern divergence zone (50°S) and branches into a coastal and oceanic part off northern Chile with the latter veering westward to merge with the SEC and the EC (Schmitz 1996, Tomczak & Godfrey 2005). The EEC flows eastward and bifurcates near the Central American coast thought to create the Costa Rica dome (CRD), a zone of enhanced productivity due to upwelling processes. Tomczak & Godfrey

(2005) assume that the equatorial current system is variable in its latitudinal location depending of large-scale climate conditions.

Strong coastal equatorward winds that arise from moisture depleted trade winds not only lead to hot and arid coastal zones and produce stable wind-driven coastal upwelling zones. Coastal watermasses that are pushed offshore through the wind-driven Ekman-transport are replaced by nutrient rich, cool depth waters that support a high primary production in the euphotic layer. This primary production fuels the production of higher trophic levels and in the end the rich fisheries in both systems (Tomczak & Godfrey 2005, Arntz et al 2006).



**Figure II-5: oceanography of the Eastern Pacific Ocean; (A) main currents (after Schmitz 1996, Tomczak & Godfrey 2005, Fiedler & Talley 2006, Kessler 2006), (B) dissolved oxygen concentration [ $\mu\text{g/l}$ ] at 400 m depth (after Stramma et al. 2008) and (C) bathymetry; AC: Arctic current; NPC: North Pacific current; CC: California current; NEC: north equatorial current; ECC: equatorial counter current; EUC: equatorial under current; EC: equatorial current; SEC: south equatorial current, PCC: Peru counter current; HC Humboldt current; SPC: South Pacific current; ACP: Antarctic circumpolar current; CRD: Costa Rica dome.**

An important characteristic of the EPO with strong impacts on the biota of the ecosystems is the pronounced oxygen minimum layer with hypoxic conditions where organisms are strongly affected or die ( $< 60$  to  $120 \mu\text{mol/l}$ ) that in some areas and depths can reach

Osuboxic ( $< 10 \mu\text{mol/l}$ ) conditions (Stramma et al. 2008, Figure II-5B). However, *Dosidicus gigas* is able to hunt in such waters (Gilly et al. 2006, Zeidberg & Robison 2007) and it has been assumed that the extension of the OMZ defines the distribution area of jumbo squid (Gilly et al. 2006).

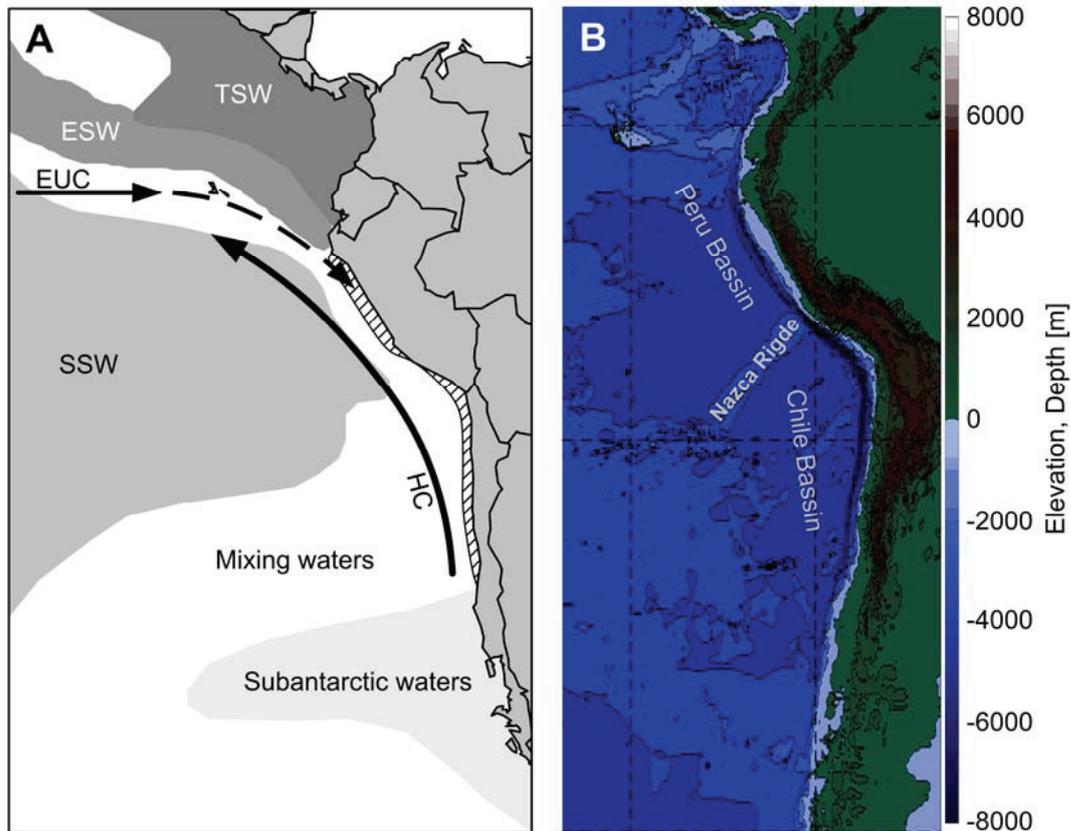
### 3.2 - The Humboldt Current System and its variability

The Humboldt Current System (HCS) covers the area off the west coast of South America from the southern divergence zone to the equator and is governed by the name-giving Humboldt Current that transport cool, subarctic waters far north (Figure II-6A). As a consequence surface water temperatures are remarkably cool when compared to other regions on similar latitudes (Chavez et al. 2008). The Humboldt Current with its coastal and oceanic branch and the counteracting southern branches of the EUC (also named Cromwell Current) together with a number of other surface and sub-surface currents determine the position and extension of the watermasses in the system (e.g. Morón 2000, Tomczak & Godfrey 2005). The main surface watermasses that among other factors determine the biotic performance (e.g. Calienes & Gullién 1981, Bertrand et al. 2004) of the Humboldt Current System are the equatorial surface waters (ESW), the tropical surface waters (TSW), subtropical surface waters (SSW), the subantarctic waters (SAW) and the important wind-driven upwelling cells that are located along the coast (Figure II-6A). A band of up to several hundred kilometres is directly influenced by the strength of the upwelling and the currents and contains the mixing waters (MW) that comprise a varying mixture of the formerly named water masses.

The shelf of the South American west coast is hardly wider than 100 km and especially in some areas in northern and southern Peru but also in north-central Chile it can be as narrow as a few kilometres before it drops into the Peru-Chile trench (Figure II-6B). The trench owes its existence to the subduction of the Nazca plate under the South American plate. In some areas the depth of this abyss exceeds 6000 m only to rise to less than 4000 m further westward in the Peruvian and the Chilean Basin that are separated by the NE-SW running Nazca Ridge off southern Peru.

In many aspects the HCS is similar to other eastern boundary current system (EBCS), the upwelling systems that are found along the west coast of the continents. It has a (1) high primary production that results from wind-driven upwelling of cool, nutrient rich waters,

(2) rich secondary production that is the basis for large biomasses of small pelagics, (3) high variability on seasonal to decadal time scales (Arntz et al 2006, Taylor & Wolff 2007) and (4) an extended oxygen minimum zone (Stramma et al. 2008).



**Figure II-6: the southeast Pacific region; (A) schematic distributions of surface water masses and important currents (after O. Morón, IMARPE, personal communication, Morón & Sarmiento 1999, Morón 2000, Tomczak & Godfrey 2005); dashed arrow indicates strengthened EUC during cool periods; hatched area: coastal zone with upwelling; TSW: tropical surface waters; ESW: equatorial surface waters; SSW: subtropical surface waters; (B) bathymetry [m] of the SE Pacific.**

Although primary productivity of the HCS is not as high as that of other EBCS, its fish production and catches are higher than that of any other EBCS and are considered to be the highest worldwide (Chavez et al. 2008) indicating an extraordinary trophic efficiency (Taylor & Wolff 2007). In some years (e.g. 1994) more than 20% of the worldwide capture production stem from the HCS (FAO 2007). Especially Peruvian anchovy and sardine but also horse mackerel, mackerel and hake since the 1950s have constantly been important for the fisheries (Wolff et al. 2003). The importance of *Dosidicus gigas* has

steadily increased since 1989 and has reached a maximum at around 600.000 t in 2005 (see Figure II-4).

Neither environmental conditions nor the primary and fishery production in the HCS are stable (Wolff et al. 2003, Arntz et al. 2006, FAO 2007). Productivity in the HCS is related to the watermasses (Figure II-6A) that shift their locations and extensions according to oscillations of larger scale climatic conditions by intensified or weakened currents in the system. Although water masses are not uniquely defined by their temperature, cooler waters are usually synonymic to nutrient-rich conditions and warmer waters represent a certain food-insufficiency that is reflected in all trophic levels (Ayón et al. 2008a, 2008b, Swartzman et al. 2008, Tam et al. 2008, Taylor et al. 2008).

Environmental variability (EV) in the HCS is pronounced and occurs in a seasonal to decadal timescale or in even longer periods. The most obvious and strongest climate oscillation besides the seasonal variations is the inter-annual ENSO that in the past occurred with a frequency of 2 to 7 years. The longer-lasting decadal oscillations are less extreme in its anomalies and often show a regime-like behaviour but nevertheless have strong impacts on the ecosystem compositions, its productivity and spatial extension (Chavez et al. 2003, 2008). Following the names of the El Niño (EN, warm conditions) and La Niña (LN, cool conditions) they have been named as El Viejo and La Vieja (the old man and old woman, respectively for warm and cool periods, Chavez et al. 2003).

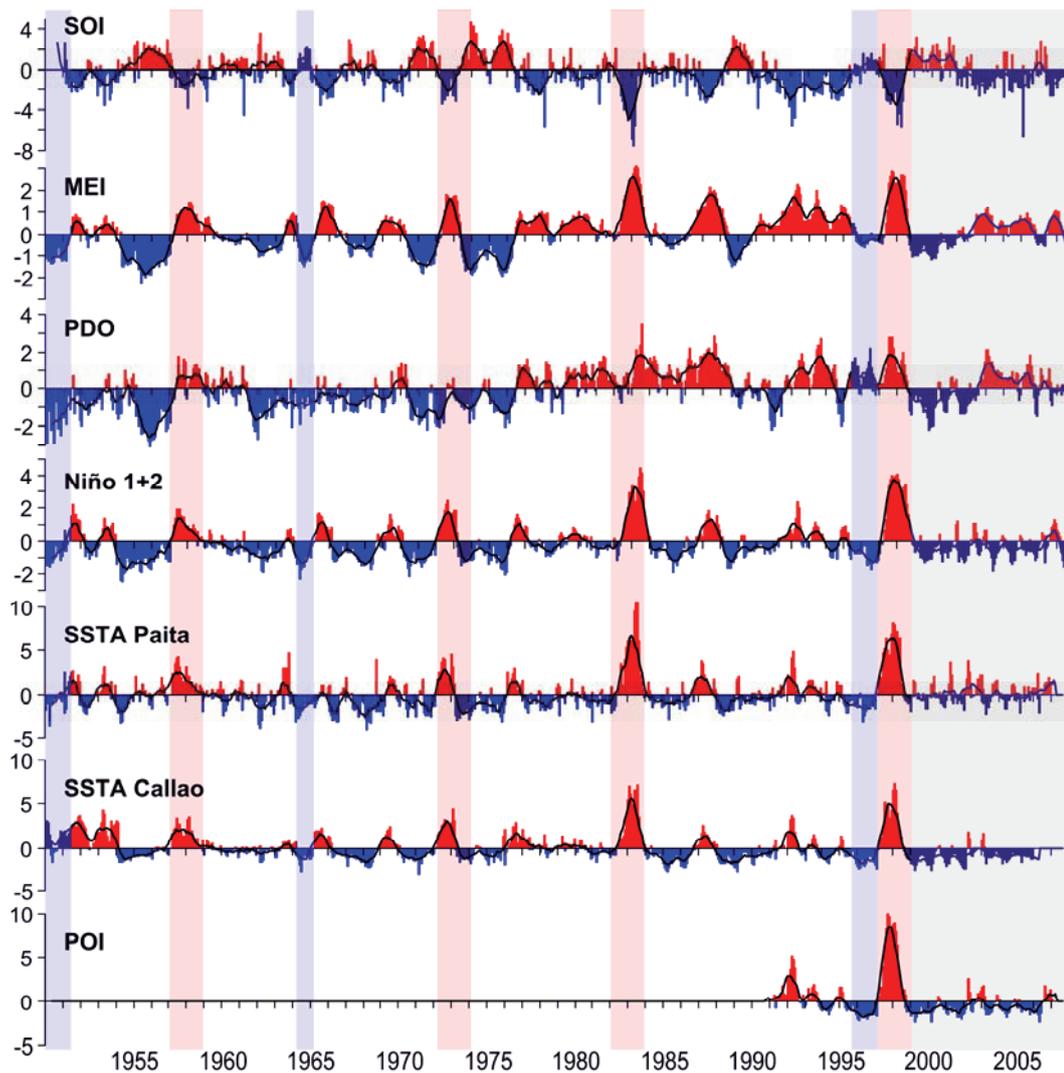
The El Niño Southern Oscillation (ENSO) with its two extremes, the climate phenomena EN and LN, is the most outstanding cause of variability in the HCS although it has been assumed early that these provoke only short term changes in the physical and biotic environment (Csirke 1988, Muck 1989). Many larger-scale changes like e.g. the early 1970s collapse of the anchovy fishery started before a respective EN. The anchovy and sardine populations and their fisheries show opposing trends that are attributed to long-term decadal oscillations of environmental conditions (Alheit & Bernal 1993, Alheit & Ñiquen 2004). This antidromic behaviour of the abundance and fishery yields of different small pelagic species on a decadal timescale has been observed worldwide (Lluch-Belda et al. 1989, Chavez et al. 2003). Variability on a temporally larger-scale that was found in the physic environment, populations (e.g. Lluch-Belda et al. 1989, Hare & Mantua 2000), communities (Chavez et al. 2003, Alheit & Ñiquen 2004, Ayón et al. 2008) and ecosys-

tems (Tam et al. 2008, Taylor et al. 2008) in the Eastern Pacific Ocean in general and the SE Pacific has often been seen as regimes. Regimes can be defined as periods with similar observations separated from other regimes by rapid transitional shifts much shorter than the actual periods (Palmer 1999, Mantua & Hare 2002). It is assumed that underlying gradual physical processes and mechanism are reflected in the communities that then through ecosystem interactions lead to amplified and clear observable steps (Steele 2004).

The impacts of the EN on the HCS have often been on a short-term level and more and more are seen as important in the regulation of the ecosystems in the region. It is assumed that the affected ecosystems react by adopting states specific to respective local abiotic conditions (Wolff & Mendo 2002) where the climate extremes EN and LN act as a “system reset” that allows formerly less important components of the ecosystem to flourish and to rapidly adjust the ecosystem to the changed conditions (Bakun & Broad 2003).

A great part of the environmental variability of the Eastern Pacific is assumed to originate in the ENSO (Pauly & Tsukayama 1987, Anderson & Rodhouse 2001, Tomczak & Godfrey 2005). During EN-events the decreasing trade winds reduce upwelling intensity, surface water warming, thermocline deepening and following lower primary production due to less nutrients in the water and lower overall production of subsequent trophic levels and fishery. Additionally, mesoscale eddies and current meanders vary. The variability of the ENSO-frequency that has been observed, is assumed to be the result of decadal to centennial oscillation in the basin and world-wide (Rajagoplan et al. 1997) but little is known about underlying mechanism of decadal-scale oscillation that are observed in the region and the basin. The strength of the important equatorial undercurrent (EUC) is closely related to the ENSO (Kessler 2006) and influences the waters of the northern HCS. The EUC in interaction with the strength of upwelling and the Humboldt Current is thought to be determining the southern extension of EN-events (Dewitte et al. 2003).

Temporally the variability is caught in timeseries of environmental variables and a number of climatic indices that try to capture an overall picture of the conditions of the region by incorporating various variables (Figure II-7). They are often including also a spatial component. It has been assumed that the indices that per se incorporate a number of highly complex factors can be imagined as a “package of weather” that captures well equally complex biological mechanisms (Stenseth et al 2003).



*Figure II-7: timeseries of multivariate indices and environmental variables with explication power for environmental conditions of the HCS; red highlighted: strong and very strong El Niño-events, blue highlighted: strong La Niña-events; grey highlighted: long lasting La Niña (i.e. La Vieja) in the northern part of southern hemisphere from 1999 to present; SOI: Southern Oscillation Index; MEI: multivariate ENSO Index; PDO: Pacific Decadal Oscillation; Niño 1+2: integrated sea surface temperature anomalies (SSTA) of 0°-10°S, 80°W-90°W; all data from <http://www.cpc.noaa.gov>; SSTA Paita (northern Peru) and Callao (central Peru) from IMARPE; POI: Peruvian Oscillation Index from S. Purca, IMARPE, personal communication.*

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## 4 - Environmental variability and biological response

### 4.1 - Short introduction

It is long-known that biological entities on all levels are dependent of abiotic factors of their habitats (e.g. van't Hoff 1901, Blackman 1905) and even the law of the minimum of von Liebig (1855) has to be interpreted in that sense. The effective abiotic variables of the marine environments are the result of regionally and globally interacting climatic forces of meteorological and oceanographic origin. Variability of factors like sea surface temperature (SST), salinity, sea level height, upwelling and oxygen content has been correlated early to the performance of exploited marine populations (e.g. Hjort 1914, Carruthers 1938; Rae 1957) and in the last decades a myriad of work empirically relating biology to its abiotic environment and its oscillations have been published (with regard to EPO and the SE Pacific e.g. Wolff 1985, 1987, Arntz & Fahrbach 1991, Hollowed & Wooster 1992, Hare & Mantua 2000, Rodhouse 2001, Lluch-Cota 2001, Lluch-Belda 2003, Mendo & Wolff 2002, Chavez et al. 2003, Alheit & Ñiquen 2004, Wolff et al. 2007, Ayón et al. 2008). Specific examples on exploited marine resources that are strongly influenced by environmental variability (EV) are equally numerous (e.g. Lluch-Belda et al 1989, Baumgartner et al. 1992, Beamish & Bouillon 1993, Jonsson 1994, Schlesinger & Ramankutty 1994, Hare & Mantua 2000)

However, understanding of the exact mechanism is difficult (Stenseth et al. 2003) and very often the length of biological timeseries does not cover a complete range or cycle of the relative climatic and environmental oscillations (McGowan et al. 1998). Additionally, the spatial aspect of the problem and the impact of fisheries may be crucial and add to the already complex problem (Bremner et al. 2006).

The impact of EV on biota can be divided into two major parts: (1) directly on the individual level through physiologic and reproductive processes and (2) indirectly through the

ecosystem (Stenseth et al. 2002). It impacts all trophic levels of the marine ecosystems and is found in all regions and latitudes. It affects abundance, mortality, fecundity and recruitment of phytoplankton, zooplankton and fish of lower trophic levels as well as apex predators like sharks, marine birds and mammals (Loeb & Rojas 1988, Alheit & Bernal 1993, Higgins et al. 1997, Clark et al. 1999, Blenckner & Hillebrand 2002, Daskalov et al. 2003, Lehodey et al. 2003). Often apparent direct relations between environmental factors and biological entities are indirect and lead to the problem of changing relationships when revised under different conditions (Myers et al. 1998, Daskalov et al. 2003)

On the ecosystem level additional dimensions (i.e. independent variables) accrue from intra-specific and inter-specific interactions. Examples are predation and competition for food and space (Ottersen et al. 2001). These can be extremely important in the emergence of ecosystem states that after an initial impulse may appear independent from exogenous influences due to feedback mechanisms (e.g. similar to the classic example of Mann 1977, Elner & Vadas 1990) and/or show considerable lags between cause (or causes!) and effect that make detection of dependencies difficult. Examples here are the lagged predator-prey interaction (Krebs 2002) and the temporal and spatial offset between primary production and zooplankton predation in upwelling areas (Botsford et al. 2003). Another example is the Russell-cycle that describes the cyclic change of macroplankton in the English Channel close to Plymouth in response to environmental conditions (Russell 1967) defined by a number of abiotic and biotic factors (Cushing & Dickson 1976). The already mentioned anticyclical behaviour of clupeid species is also assumed to be the result of interaction between the species in the temporal and spatial environmental context (Cushing 1982, Lluch-Belda 1989, Chavez et al. 2003).

The identification and understanding of complex interactions between intrinsic and extrinsic factors influencing individuals, populations and ecosystems originating in EV requires the joint effort of ecologists, climatologists and statistical modellers (Stenseth et al 2002). In the following section a number of examples of interactions are presented from the marine realms and/or when possible with relevance for the HCS and the present thesis.

## **4.2 - Interactions between environmental variability and biological response**

Temperature is an important and often dominating factor for mechanisms on the physiological level. Dependence of water temperature were found for individual growth and other individual vital rates (e.g. DeYoung et al. 2004, Jacobson et al. 2005), higher metabolism that can result in changes of predation levels (Bogstad & Gjørseter 1994), natural mortality (Pauly 1980) and decreased incubation period and maturation that result in lower egg and larval mortality (Skud 1982, Smith 1995, Wolff et al 2007). The mismatch hypothesis of Cushing (1982) related spawning and egg and larval survival to a number of environmental variables and their interactions.

The effects of EV on the population level are more complex and published links often describe indirect mechanisms that in the end again base in physiology. Examples for this are the association between temperature and recruitment numbers (Ware 1991, Chen & Ware 1999, DeYoung et al. 2004, Jacobson et al. 2005), survival rates (Cisneros-Mata et al. 1996) and spatio-temporal dynamics of populations (Bjørnstad & Grenfell 2001). An example for a relative direct link between EV and biological response on the population level is larval transport. Other observations like availability of food, population growth (DeYoung et al. 2004) and carrying capacity (Jacobson et al. 2005) that were found to be linked to EV can already be seen to be the result of inter-specific relations in the communities or with fisheries (Fréon & Yáñez 1995).

Exact mechanism of the effects of environmental factors on communities and their ecosystems as such are difficult to detect and changing spatial connectivity are important for the interactions between different populations (DeYoung et al. 2004, Alheit 2007). It regulates the frequency of encounters (Collie & Spencer 1994) as well as competition for space and food. It has been proposed that dominant species of an ecosystem respond to environmental factors, whereas subdominant ones respond only to the dynamics of the dominant ones (Skud 1982) but this can be questioned. Ecosystems adjust to EV by changed organization and abundances of entities that change the significance of inter-specific interactions. As a result, specific states emerge that are related to particular environmental conditions (Tam et al. 2008, Taylor et al. 2008a) that can optimize the efficiency of energy flows according to the environmental conditions (Tam et al 2008).



## CHAPTER III: Hypothesis

### 1 - A hypothesis on range expansion and spatio-temporal shifts in size-at-maturity of jumbo squid (*Dosidicus gigas*) in the eastern Pacific Ocean

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Published in CalCOFI Report

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Keyl F, Argüelles J, Mariátegui L, Tafur R, Wolff M, Yamashiro C (2008) A Hypothesis on Range Expansion and Spatio-Temporal Shifts in Size-at-Maturity of Jumbo Squid (*Dosidicus gigas*) in the Eastern Pacific Ocean. CalCOFI Rep 49:119-128

## 1.1 - Abstract

*Dosidicus gigas* is a fast growing predator of the eastern Pacific Rim with a high energy demand. Since 2000, it has been found in waters beyond its until then known northern and southern distribution limits. At the same time, specimens in the southern hemisphere were observed to reach maturity at significantly larger sizes. Spatiotemporal differences in temperature and food abundance may explain population changes in maturation, growth, and migration. Size-at-maturity depends on temperature and food availability, meaning jumbo squid will mature at smaller sizes under warm conditions and at larger sizes that can migrate longer distances in cool conditions. In this paper, we present the hypothesis that the present invasion of jumbo squid into formerly uninhabited areas was the result of a combination of favourable environmental conditions and fishery impacts: the regime shift from warm to cool water following a strong La Niña/El Niño combined with the fisheries' impact on competitors and predators of *D. gigas* opened up a previously unavailable niche, or "loophole" and allowed for the present spatial expansion of jumbo squid.

## 1.2 - Introduction

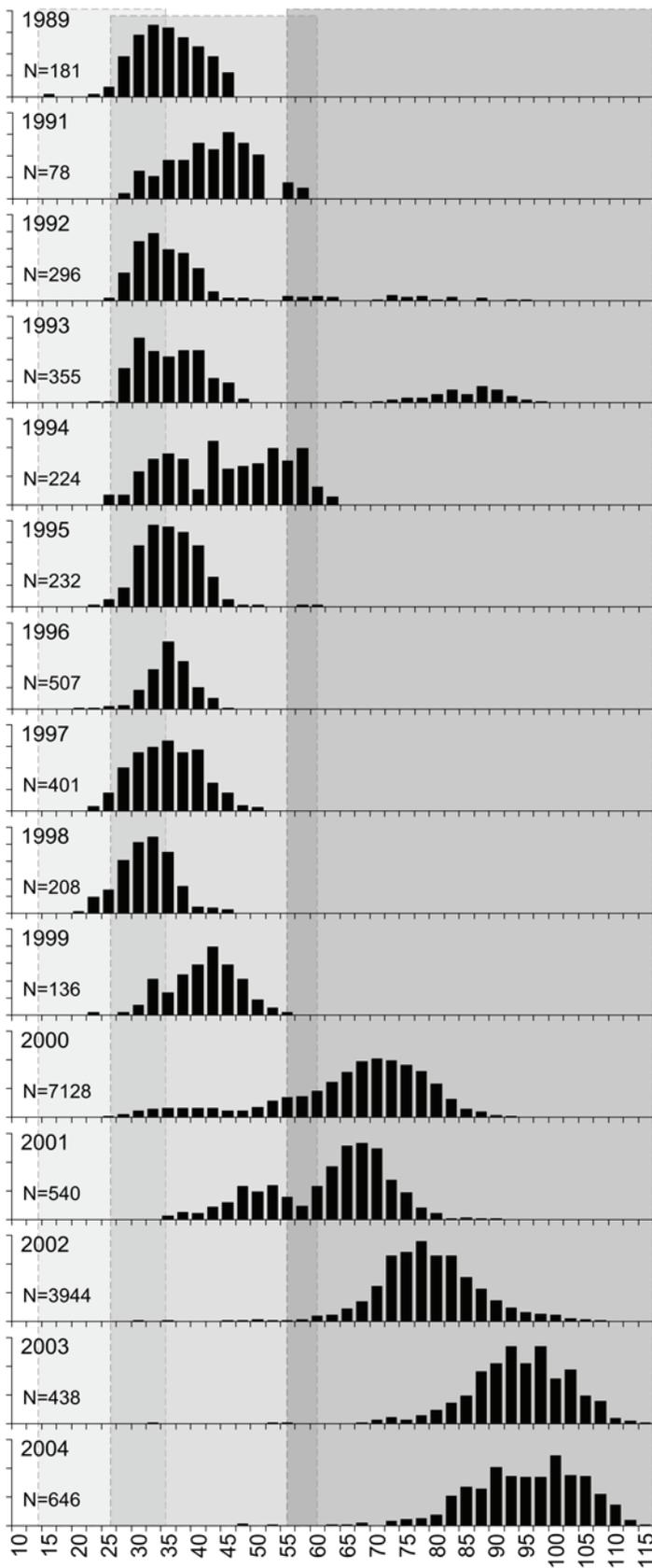
The jumbo squid, *Dosidicus gigas*, is a migratory and voracious predator of the eastern Pacific Ocean with high abundances in the southern area of the California Current system and in the northern region of the Humboldt Current system (Roper et al. 1984). It has a high energy demand that is satisfied by unspecific feeding upon prey items that are 5% to 25% the size of its dorsal mantle length (ML), although bigger prey have been reported. In cannibalistic feeding, a commonly observed behaviour for jumbo squid, prey size may reach up to 87% of the predators' ML (Markaida & Sosa-Nishizaki 2003). Jumbo squid hunt in small groups (Nigmatullin et al. 2001) and, although they are extreme generalists, it has been shown that myctophids and euphausiids often comprise an important percentage in the diet of juveniles and adults (Markaida 2006a, Blasković et al. 2007). Large females can have as many as 32 million eggs (normally 0.3–13 million eggs are found), which is the highest fecundity among cephalopods (Nigmatullin et al. 2001). Although not universally accepted (Masuda et al. 1998), *D. gigas*, like most other cephalopods, is thought to exhibit "cephalopod senescence" (Anderson et al. 2002) and is semelparous, that is, it does not regress developed reproductive organs but dies after the first spawning or the first spawning sequence (Nigmatullin et al 2001). Like other cephalopods, it does

not develop a true larval phase but hatches after three to 10 days as a paralarva (Yatsu et al. 1999), a life stage very similar to the subsequent adult stage. Jumbo squid have a monthly growth rate of up to 8 cm in mantle length (ML) during the paralarvae and the following juvenile stages, and grow up to 6 cm per month in later stages. This is the highest growth rate reported for all cephalopod species (Nigmatullin et al. 2001, Markaida et al. 2005) and enables jumbo squid to reach the reported maximum mantle lengths of up to 120 cm in a lifespan of just a few to 18 months (Nigmatullin et al. 2001).

Until the end of the last millennium, the jumbo squid's northern and southern distribution limits were found at around 30°N and 40°S, with the highest abundances located in the Gulf of California and in waters off Peru (Nigmatullin et al. 2001). A recent RAPD-genetic analysis of eight locations in Mexico, Peru, and Chile indicated that the jumbo squid subpopulations from the two hemispheres are genetically separated, probably because the equatorial currents and counter-currents form a natural barrier (Sandoval-Castellanos et al. 2007).

Various traits of its life history, like shifts in size-at-maturity, cannibalism, and range expansion, give *D. gigas* an extremely plastic response to the highly variable oceanic habitats within the eastern boundary upwelling systems.

Jumbo squid size-at-maturity is highly variable and several authors (e.g. Nesis 1983, Nigmatullin et al. 2001) have proposed three different size-at-maturity strategies in its distribution in the eastern Pacific Ocean (EPO): a group found in the center of its EPO distribution that matures at a small size; a group throughout the whole distribution area that matures at a medium size; and a group in the northern and southern distribution limits that matures at large size. In Peruvian waters, these groups have not yet been identified from the available oceanic industrial and coastal artisanal fisheries data. Only a small-maturing group and a large-maturing group, which generally correspond to the medium- and the large-sized groups classified by Nigmatullin et al. (2001), can be distinguished (fig. 1) and appear to be both spatially and temporally separated (Argüelles et al. 2008). The terms “small” and “large” in the present study refer to the two size-at-maturity groups found in the Peruvian waters; when we refer to Nigmatullin et al.'s (2001) group classification, this is explicitly mentioned. In the Peruvian exclusive economic zone (EEZ), from 1989 through 1999 (except 1992–93) only specimens of the small size-at-



*Figure III-1 Occurrence of sizes (ML [cm]) of mature females caught by industrial jig fishery in the Peruvian EEZ; shaded boxes indicate the three groups of size-at-maturity proposed by Nigmatullin et al. (2001); modified after Argüelles et al. (2008).*

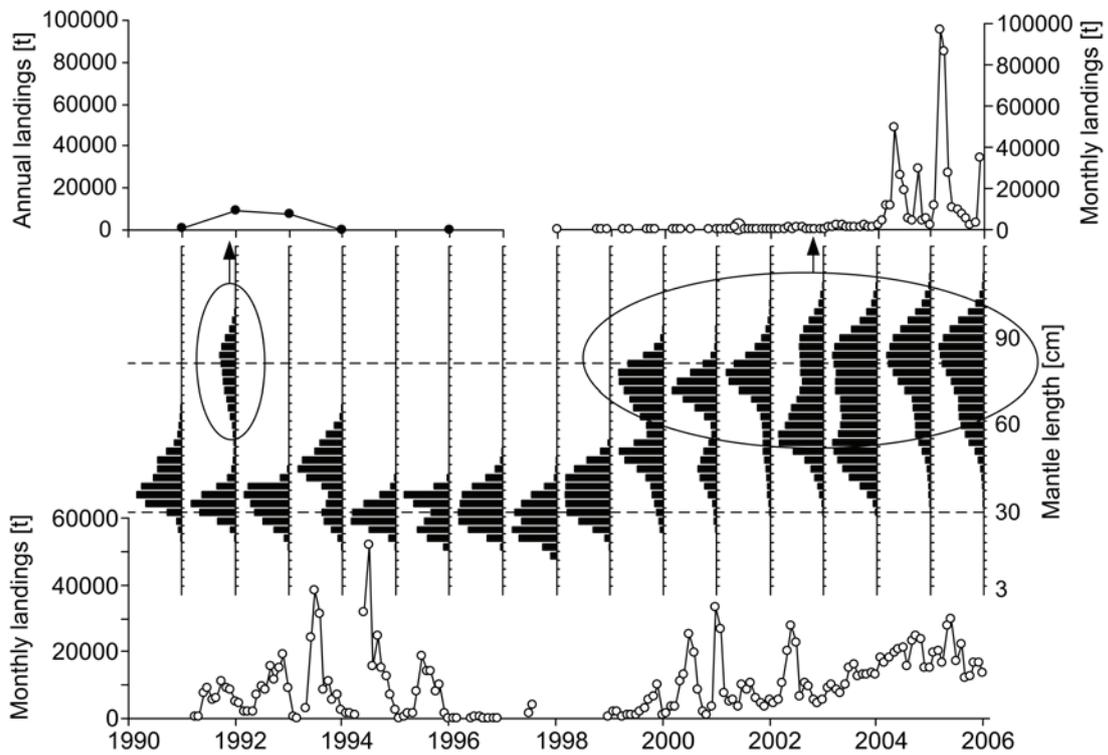
maturity group were caught, whereas, after a transition period in 1999–2000, only specimens thought to belong to the large group were caught (Figure III-1).

Statolith analyses revealed that the longevity of mature individuals collected by observers in the industrial fishery in the Peruvian EEZ ranged from around 120 to 350 days according to their size (Masuda et al. 1998, Argüelles et al. 2001). A temporal change in size-at-maturity has also been found for the jumbo squid population in the Gulf of California, where, in a three-year period after the 1997–98 El Niño, the size-at-maturity varied considerably from large to small or medium (Markaida 2006b, Bazzino et al. 2007). Although these groups may belong to genetically different subpopulations (Nesis 1983), no work has been published on the origin or an underlying cause for the existence of these groups.

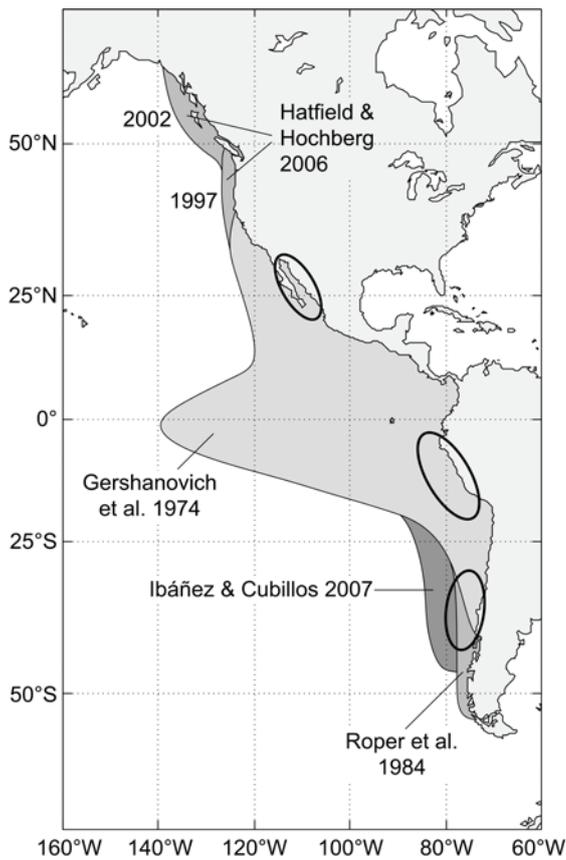
Cannibalistic feeding is a common behaviour among cephalopod species (Amaratunga 1987) and this has been confirmed in stomach content analyses of *D. gigas* from the Gulf of California (Markaida 2006a) and Peruvian waters (Blasković et al. 2007). Among other things, cannibalism reduces intraspecific competition for food and mating under conditions of reduced food availability or very high population densities, allows larger specimens to maintain their food intake over time, and therefore, to increase their fitness (Polis 1981). The cannibalistic weight percentage of all stomach contents of specimens caught by the industrial fishery on jumbo squid in Peruvian waters in the years from 2004 to 2006 ( $n = 1930$ ; 30–112 cm ML) reached 75% (IMARPE unpublished data). Although this high rate of cannibalism may be partly due to stress during fishing (Markaida & Sosa-Nishizaki 2003, Ibáñez et al. 2008) and although it may reflect a systematic bias because only larger individuals were captured, it suggests a “population energy storage” strategy: energy is built up during favourable ecosystem conditions by increasing the number of individuals that can be reduced again by the larger individuals when the population is under ecological stress.

After the 1997–98 El Niño, a range expansion of jumbo squid was observed in the north Pacific Ocean (Zeidberg & Robison 2007, Staaf et al. 2008) and south Pacific Ocean (upper panel of Figure III-2; fishery data of Chilean SENARPESCA, see web page: <http://www.senarpesca.cl/>). From 2002 to 2004, reported annual landings of jumbo squid from off Chile increased from 5500 t to nearly 300,000 t. This increase in landings par-

tially resulted from the directed artisanal jig fishery for jumbo squid, but squid was mainly captured as increased bycatch of other fisheries employing different types of fishing gear (Ibáñez et al. 2008). After mass strandings in California in 2002 and sightings of *D. gigas* up to Alaska since 2002, the jumbo squid became an important target of the U. S. sport fishery (Hatfield and Hochberg 2006). This coincides with the steadily increasing biomasses as estimated from catch per unit of effort (CPUE) and acoustic surveys (IMARPE, unpublished data) which have sustained the continuously increasing total allowable catch for the Peruvian fishery since 2000 (lower panel of Figure III-2). At present, the northern and southern limits of jumbo squid distribution are 60°N and 50°S, respectively (Figure III-3), although it is not clear if the expansion has ceased or will continue into new areas.



**Figure III-2** Temporal coincidence of high annual landings in Chilean regions IV (Coquimbo, ~30°S) to VIII (BíoBío, ~40°S, upper panel; filled circles: annual landings from 1991 to 97, open circles: monthly landings from 1998 to 2005) with the occurrence of the large specimen observed in the landings from the Peruvian EEZ in 1992 and from 2000 on (middle panel); lower panel: monthly landings of industrial and artisanal fishery in the Peruvian EEZ.



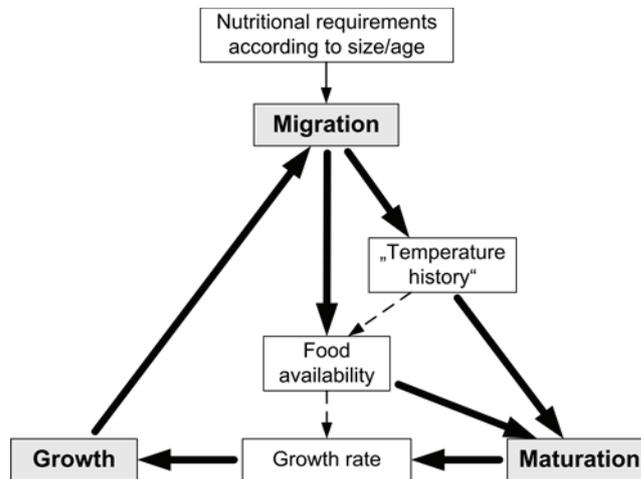
*Figure III-3 Distribution area of jumbo squid according to different sources in different years indicating an extension of the range; ellipses show main fishing areas.*

### 1.3 - The functional triad migration-maturation-growth

Because changes in population size structure, abundance, and distribution observed during the last decade seem to be related (Figure III-2), we propose that individual migration, maturation, and growth are connected via a functional triad on a physiological and energetic basis: as a mobile and fast growing hunter, *D. gigas* has a high energy demand and available food has to change rapidly in quality and size while it grows from the planktonic paralarva to its final length in just a few months. Migration routes must thus change with the spatiotemporal occurrence of prey items as the nutritional needs of the squid change through different size classes.

During the horizontal migration of up to 30 km per day (Gilly et al. 2006) and regular vertical migrations to depths of 1200 m (Nigmatullin et al. 2001), individuals pass through different water masses which leads to a unique temperature and nutrition history for each squid. We postulate that this history may govern the onset of jumbo squid matu-

ration by a specific, but unknown number of day-degrees, as has been suggested for other cephalopods (Rodhouse 1998). Environmental variables, temperature, and food availability have also been described as factors that control cephalopod maturation. High nutrition levels and low temperatures are known to cause late maturation and low nutrition levels and high temperatures cause early maturation (Mangold 1987). Following this reasoning, the individual temperature and nutrition history would thus determine the onset of maturation, which in turn controls the maximum size the individual can attain (Figure III-4) because *D. gigas* is semelparous and dies after its first reproduction season (Nigmatullin et al. 2001). Consequently, groups of *D. gigas* that differ in size-at-maturity and final size may have experienced different environmental conditions with respect to temperature and nutrition and may have therefore migrated along different routes.



**Figure III-4: Scheme of the functional triad migration-maturation-growth: individual nutritional requirements lead to migration patterns that lead to a temperature history according to water masses passed, which controls the onset of maturity that in turn controls growth rate and finally growth. Growth, i.e., the size of a specimen, again influences its migration; dashed interactions that have been reported for some cephalopod species (e.g., Pecl & Jackson 2006) have not been considered in the present hypothesis; further explanations in the text.**

In Peruvian waters, the available data for mature females indicate that there are two size-at-maturity groups and do not support Nigmatullin et al.'s (2001) three-group hypothesis (Figure III-1). The size distributions of immature and mature females and males in Peruvian landings suggest the existence of more groups in the population (Figure III-2, middle panel). However, since these landings are composed of mature and immature individuals of possibly different cohorts (Tafur et al. 2001) they should not be confused with the dif-

ferent groups of size-at-maturity. Argüelles et al. (2001) found that individuals of the large size-at-maturity group are older than those of the small group, which agrees with our hypothesis.

### **Size-at-maturity groups**

Very few studies have examined whether genetic, abiotic, biotic, or a mixture of these factors are responsible for observed differences in sizes-at-maturity of jumbo squid (Nesis 1983, Nigmatullin et al. 2001). This suggests that the underlying mechanism proposed in our study, which links physiological and ecological/environmental factors, has not been considered.

If, as the Peruvian fishery data suggest (Figure III-1 and Figure III-2), mature specimens were divided into small/early and big/late maturing groups, the small group would be at a disadvantage since the higher *relative* energy a small individual invests into reproduction yields a lower reproductive output (Pecl and Jackson 2006, Argüelles & Tafur 2007). Additionally, small individuals have no access to larger prey or conspecifics at higher trophic levels, as do the larger specimens. On the other hand, smaller individuals may benefit under conditions of low food availability, as individually they invest less *absolute* energy into reproduction and because they are capable of feeding on smaller, more numerous food items at lower trophic levels. An advantage of the small size-at-maturity group is also its shorter generation time, so that lower individual reproduction adds up to a high population reproduction per unit of time. Moreover, the higher population turnover rate decreases the mean trophic level of the population as small individuals predominate, allowing it to feed at the more productive lower trophic levels.

Based on the above, we propose that the two groups have opposite life history responses to two basic ecosystem conditions of the Humboldt Current system (HCS). The small size-at-maturity strategy ensures that the population survives during warm periods with low food availability, while the big size-at-maturity strategy allows for maximizing individual fitness during cool periods with abundant prey.

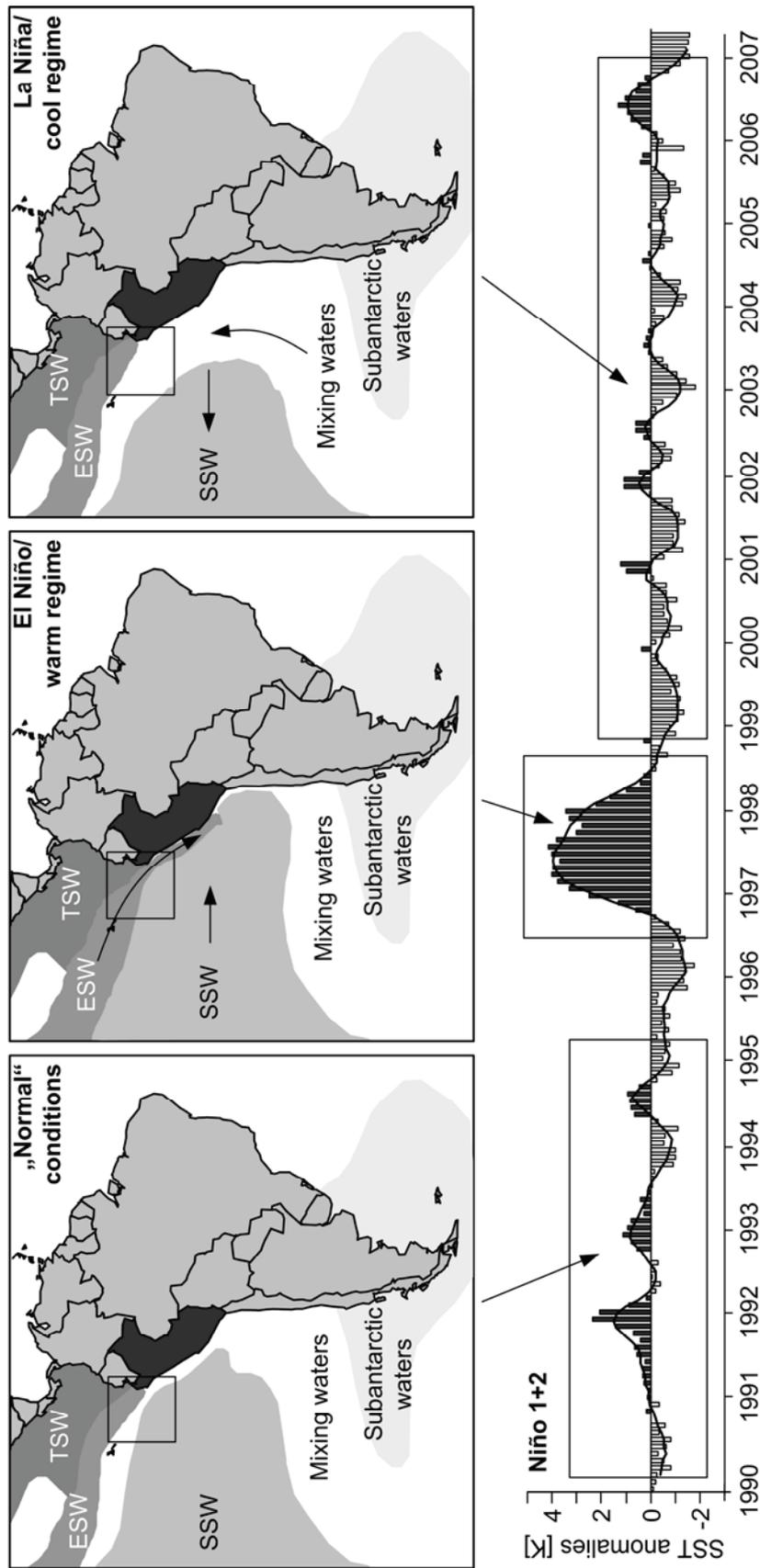


Figure III-5: Schematic illustration of the “mean” location of water masses during different times/regimes in the South Eastern Pacific obtained from satellite SST data and oceanographic data collected during research and monitoring cruises of the IMARPE (after Morón & Sarmiento 1999; Ahumada et al. 2000; O. Morón, IMARPE, pers. commun.); ESW: equatorial surface waters; TSW: tropical surface waters; SSW: subtropical surface waters; the squares in the sketches show the Niño 1+2 region; lower panel shows SST anomalies of the Niño 1+2-region.

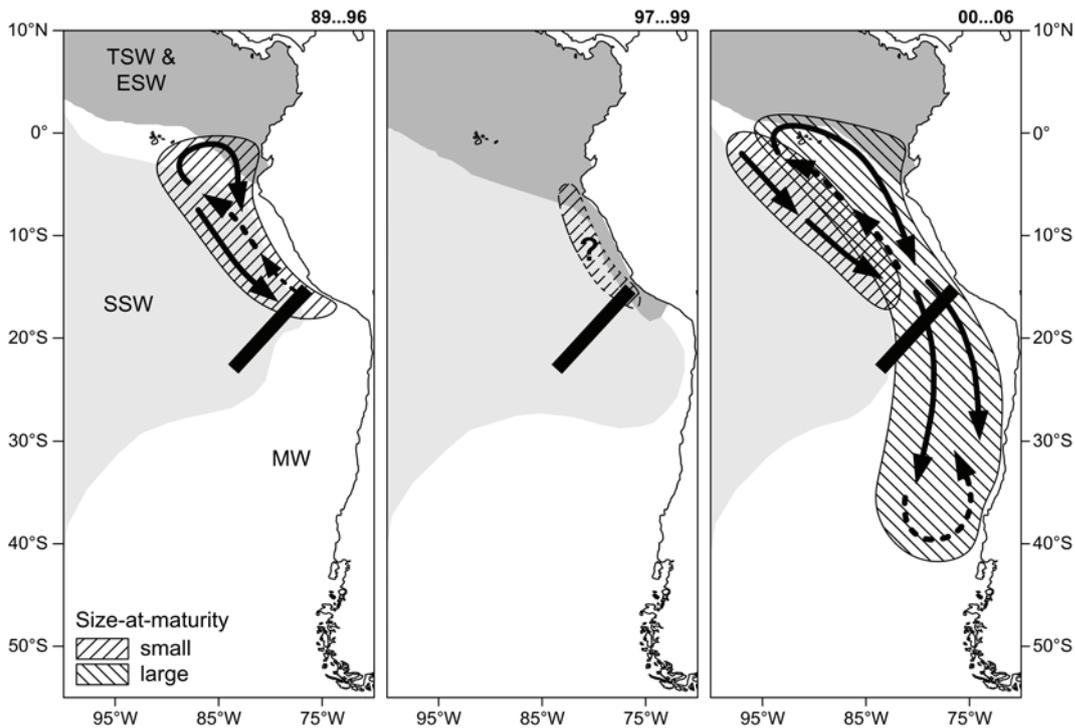
### **Migration pattern and observed range expansion**

In the HCS these conditions are related to water masses characterized by different sea surface temperatures (SST) and salinities that change their locations off the coast of Peru according to large-scale oceanographic and atmospheric conditions and the resulting intensification or weakening of currents (Figure III-5). In the 1990s until the beginning of 1996, the EPO showed moderate changes between positive and negative SST anomalies, which resulted in the limit between cool mixing waters (MW) and warmer subtropical surface waters (SSW) occurring inside the Peruvian EEZ. During the strong El Niño of 1997–98 the equatorial undercurrent (EUC) increased in strength, transported very warm equatorial surface waters southward, pushed the SSW closer to the Peruvian coast, and weakened the highly productive coastal upwelling cells. From 1999 on, a general cool regime entered the eastern Pacific Ocean, characterized by intense upwelling, a strong Humboldt Current and weak EUC. It produced negative SST anomalies in the Peruvian EEZ by pushing the limiting SSW farther westward and outside the Peruvian EEZ, and by allowing the formation of a broad zone of cool, nutrient-rich MW off the Peruvian coast (Morón & Sarmiento 1999, O. Morón, IMARPE, pers. commun.).

We assume that changes in water mass distributions lead to changes in the distribution area and main fishing grounds of *D. gigas* (Figure III-6). The small size-at-maturity group found in the official landings data for the early 1990s is assumed to be associated with the boundary between the cool MW and warmer SSW and to move back and forth between the two water masses. Migration to the southern part of the HCS during that period seems to be restricted to some years and a low number of individuals. Although exact mechanisms are not known, this may result from the location of the SSW relative to the Nazca Ridge (black bars in Figure III-6) that possibly acts as a barrier for smaller *D. gigas*, preventing them from migrating to colder waters in the south. This barrier may have its origin in bathymetric and oceanographic conditions different from those farther south and farther north off the Peruvian coast (Wolff et al. 2003, Shaffer et al. 2004), leading to significantly weaker upwelling and to less productivity in coastal areas farther south (Longhurst 1995).

Further evidence for this is found in the data from the industrial fishery inside the Peruvian EEZ which indicate that the resource is mainly distributed north of the Nazca Ridge (Taipe et al. 2001). With DMSP-OLS images it is possible to assess night-time activities

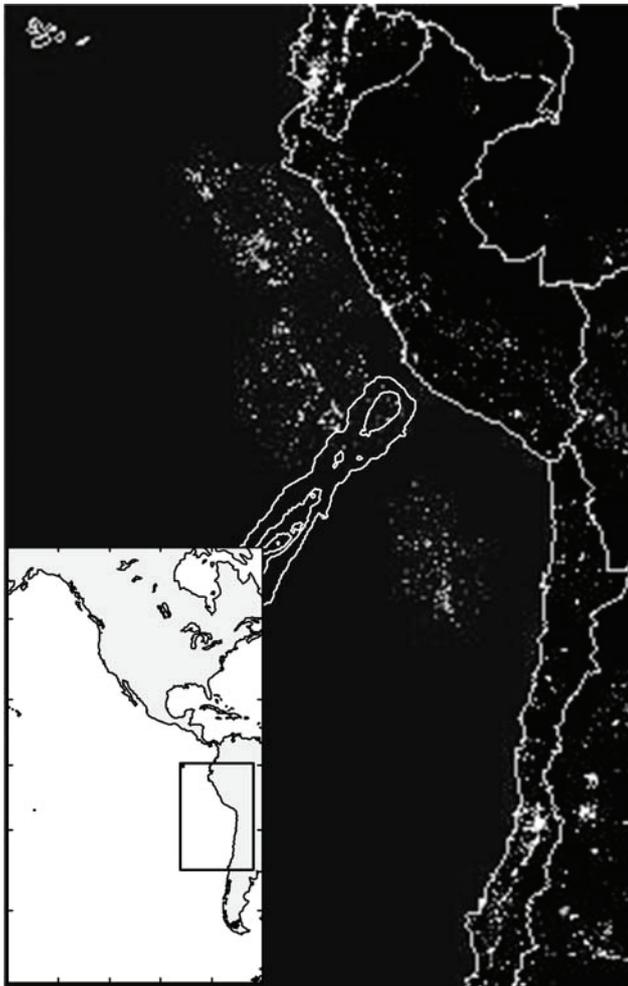
of the industrial jumbo squid jigging fleets as they use strong lights to attract their target (Waluda et al. 2004). A night-time light image integrating the cloud-free nights in 2003 (Figure III-7) shows that just south of the Nazca Ridge no jig fishery has occurred this year.



**Figure III-6: Scheme of distribution areas/fishing grounds and proposed migration routes of *D. gigas* in the SE Pacific during the “normal” period from 1989 to 1996, during and after El Niño 1997 to 1999 and from 2000; hatched areas: distribution areas/fishing grounds of *D. gigas*; black arrows: assumed migration patterns of *D. gigas*; broken black arrows: assumed paralarval movement; dark grey area: tropical and equatorial surface waters (TSW & ESW); light grey area: subtropical surface waters (SSW); black bars: sketch of Nazca Ridge.**

Since 1999, the size of the individuals in the landings reported to Peruvian authorities increased due to the displacement of the limit of the two water masses farther offshore and outside the Peruvian EEZ (Figure III-5). Inside the Peruvian EEZ the cool, nutrient-rich MW were found, and with these the big size-at-maturity group developed that was reported to national Peruvian fishery authorities. Since then, the limit between the warmer SSW and the cooler MW has been outside the 200mile border and, according to our hypothesis, the small size-at-maturity group should be found there. Night-time satellite images suggest that the international jigging fleet has been operating outside the EEZ at all

times (Waluda et al. 2004, IMARPE, unpubl. data) but no data on catches and population structure are available. Preliminary investigations of more recent night-time images at IMARPE and the night-time lights image of 2003 (Figure III-7) suggest that the bigger part of the total industrial fishing effort is applied outside the EEZ.



*Figure III-7: Integrated night-time lights image of 2003 basing on visible and infrared radiation satellite data; white points off Peru and Chile indicate lights employed during night time fishing activity of the industrial jig fishery (modified after National Geophysical Data Center; <http://www.ngdc.noaa.gov/dmsp/>); Nazca Ridge is shown by depth lines in 1000 m intervals.*

Preliminary results from IMARPE's October–November 2007 research cruise, 0710–11, support this hypothesis. During the survey that covered the east-west trajectory from 30 nm to 350 nm off the northern Peruvian coast (4°S to 8°S), all mature individuals (72 to 98 cm ML;  $n = 5$ ) fished by trawl net and manual jigging inside the EEZ belonged to the large size-at-maturity group, and those outside it (22 to 42 cm ML;  $n = 18$ ) to the small group. This suggests that the large size-at-maturity group occurs mostly inside the EEZ and the small size-at-maturity group outside the EEZ because of the new water mass distribution. We propose that larger animals are restricted from reaching the warmer waters now found outside the EEZ because they require higher nutrition levels than these waters

can provide. Individuals of the small group moving to cooler water masses inside the EEZ become part of the large size-at-maturity group as a consequence of the conditions of their new environment. This leads to a separation of the two size-groups that helps small individuals avoid falling prey to larger conspecifics.

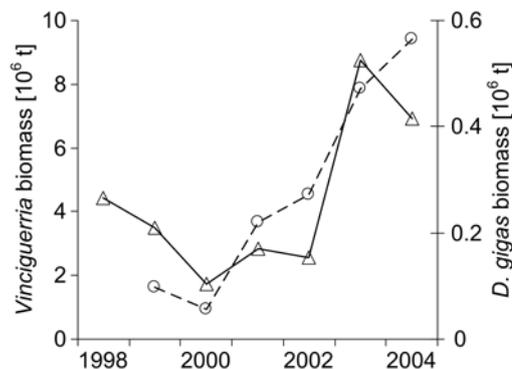
The barrier formed by the Nazca Ridge and the water-masses ceases to exist with the retraction of the SSW from the coast, enabling parts of the population to migrate upstream along the Humboldt Current to Chilean waters. In the area from 30°S to 40°S where the Humboldt Current departs from the Chilean coast, they become vulnerable to fisheries again and are caught in large quantities. Clarke & Paliza (2002) proposed that mature jumbo squid may spawn in this area, but to our knowledge no one has yet reported paralarvae in Chilean waters. It is unknown whether spawning occurs in this area, or if the same individuals return to warmer waters off Peru to spawn, or die without spawning. However, periodic mass strandings in southern Chile have been reported (Ibáñez & Cubillos 2007). Few jumbo squid are fished in waters off northern Chile inside the EEZ (SENARPESCA data), however, in 2003 the international jigging fleet operated outside the EEZ (Figure III-7). Again, the exact reason for this remains unclear but may result from the environmental conditions mentioned before. The changing intensities of the oceanic and a coastal branch of the northward flowing Humboldt Current in this area in different periods (Blanco et al. 2002) may also contribute to the observed distribution patterns.

#### **1.4 - Range expansion of *D. gigas*: why now?**

Although jumbo squid have never before been sighted as far north as Alaska, nor has the Chilean fishery reported such high landings as since 2003, range expansions have been observed before in both hemispheres (Hatfield & Hochberg 2006, Ibáñez & Cubillos 2007, Staaf et al. 2008). Thus the question arises why the present range expansion is so much stronger. We assume that both environmental variability and the indirect effect of fishery pressure in the HCS and the CCS affect the range expansion.

The last decade has seen a rare succession of environmental phenomena: after the strong La Niña/El Niño combination from 1996 to 1998, a Pacific-wide regime shift from warm to cool occurred that can be observed in the SST-anomalies off Peru (lower panel of Figure III-5). The La Niña/El Niño period is considered as a “system reset” that can allow

rapidly reproducing species to move into environmental “loopholes”, i.e. niches formerly occupied by other species (Bakun & Broad 2003). The “loopholes” in the EPO open after the La Niña/El Niño “system reset” and are exceptionally accessible for *D. gigas* because cool-regime waters are nutrient rich. At the same time, fisheries have greatly reduced the abundance of *D. gigas* competitors, such as mackerels and hake, and predators, like sharks and marine mammals (Tam et al. 2008), in the last decades (Pauly & Palomares 2005, Lotze et al. 2008), but have probably not affected their prey as euphausiids and myctophids. Thus, it seems that the concurrence of favourable “loopholes” after a “system reset” and fishery-caused reductions in competitors and predators has enabled *D. gigas* to expand its range.



**Figure III-8: biomasses of the myctophid *Vinciguerria* (triangles) and *D. gigas* (circles) in the Peruvian EEZ (IMARPE, data from acoustic surveys).**

These have been found to be important in the diet of *D. gigas* in the CCS (Markaida et al. 2006a) and the HCS (Blasković et al. 2007, Taylor et al. 2008) and can rapidly build up vast biomasses. No exploitation of the most important myctophid in the HCS, *Vinciguerria lucetia*, is known (Froese & Pauly 2007), and there are no reports of human exploitation of euphausiids in the HCS. The biomass increase of *V. lucetia* since 2000 may have partially fuelled the increased biomass of jumbo squid (Figure III-8, IMARPE unpublished data). Pauly et al. (2002) suggested that the abundance of marine resources as invertebrates and jellyfish have a strong positive response to fishery caused reductions in their competitors and predators. These groups are fast growing species often considered suppressed under “normal” conditions.

### 1.5 - Conclusion and final remarks

The proposed migration-maturation-growth triad can explain the observed changes in population structure, abundance, and distribution of jumbo squid in the eastern Pacific

Ocean during the last decade. Direct experimental evidence to prove our hypothesis is still missing, however. Until now it has not been possible to keep *D. gigas* under controlled aquarium conditions and the longest reported period that an adult jumbo squid has survived in captivity is 12 days (Gilly, Hopkins Marine Station, pers. comm.); paralarvae have been reported to survive 10 days (Ichii et al. 2002). Nevertheless, experimental work in the laboratory should be conducted to verify – or falsify – that *D. gigas* maturation and growth depend on temperature and food, which Mangold (1987) suggests for cephalopods in general. Other support for the hypothesis could come from biometric and maturity data from the Japanese and Korean jumbo squid fisheries, believed to have been operating outside the Peruvian EEZ for as long as those operating inside.

We have concentrated our analysis on the Peruvian part of the HCS, and further studies should clarify if the proposed triad also explains the range expansion and change in population size structure of *D. gigas* in the Gulf of California and the Californian Current system of the northern hemisphere, which are subjected to similar environmental and—at least in the Gulf of California —fishery conditions.

**Acknowledgements.** We kindly thank IMARPE and all our colleagues there for their generous provision of data and helpful assistance that formed the basis of this work. F. Keyl was partly financed by the EU project CENSOR (Climate variability and El Niño Southern Oscillation: Impacts for Natural Resources and Management, contract 511071). This is CENSOR publication 0339.

## CHAPTER IV: Investigative publications

### 1 - Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989–2004

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**Published in Progress in Oceanography**

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Argüelles J, Tafur R, Taipe A, Villegas P, Keyl F, Dominguez N, Salazar M (2008) Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989–2004. Prog Oceanogr 79:308-312

## 1.1 - Abstract

Changes in population structure of the jumbo flying squid *Dosidicus gigas* in Peruvian waters were studied based on size-at-maturity from 1989 to 2004. From 1989 to 1999, mature squid belonging to the medium-sized group prevailed, but from 2001 on, mature squids were larger. This change is not related to the changes in sea surface temperature and we hypothesize that it was caused by the population increase of mesopelagic fishes as prey.

**Keywords:** *Dosidicus gigas*, Length-at-maturity, Population structure, Peru

## 1.2 - Introduction

The jumbo flying squid *Dosidicus gigas* (family Ommastrephidae) is one of the most abundant squids in the eastern Pacific Ocean (Nesis 1970, 1983, Klett 1996, Anderson & Rodhouse 2001, Nigmatullin et al. 2001), and is distributed in the Eastern Pacific from California (USA) to Chile (Nigmatullin et al. 2001). It inhabits a wide range of epipelagic to mesopelagic habitats (up to 1200 m depth). Like other squid species, *D. gigas* is short-lived with a longevity of about 1 year (Arkhipkin & Murzov 1986, Masuda et al. 1998, Argüelles et al. 2001, Markaida et al. 2004) with highly labile populations that exhibit large fluctuations in abundance in response to environmental variability (Waluda et al. 2006). *D. gigas* is an important opportunistic predator in the pelagic ecosystem of the southeastern Pacific Ocean (Nesis 1970, 1983). Myctophid fish compose a large portion of its diet but *D. gigas* also preys on hake, anchovy, mackerel, crustaceans, squid and other organisms (Shchetinnikov 1986, 1989, Markaida & Sosa-Nishizaki 2003, Markaida 2006, Field et al. 2007).

Off Peru, *D. gigas* has been targeted commercially by the artisanal fleet since 1961 (Yamashiro et al. 1998), mainly in the north, and by industrial fleets since 1991 (Taïpe et al. 2001). For Chile, landing data of *D. gigas* are available since 1957 (Rocha & Vega 2003) and there are even older records of stranded individuals (Wilhelm 1954). In Chile *D. gigas* was formerly used as bait in *Genypterus* fisheries due to its very low commercial value. Catches of *D. gigas* were sporadic before 1970, although high abundances have been reported (Schmiede & Acuña, 1992). In the Gulf of California the artisanal fishery targeting *D. gigas* started in 1974 (Ehrhardt et al. 1983) but between 1983 and 1987 the

fishery disappeared, perhaps due to the recruitment failure from overfishing or unfavourable environmental conditions following the 1982–1983 El Niño event (Klett 1996).

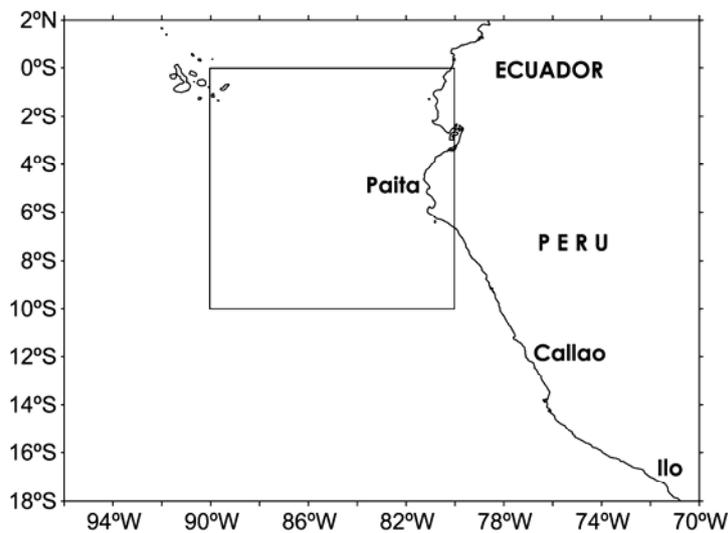
The population structure of *D. gigas* is difficult to be assessed due to variability in length-at-maturity. Three sizes of sexually mature squid were defined by Nigmatullin et al. (2001) on the basis of the mantle length (ML) of adult males and females: a small-sized group (13–26 cm and 14–34 cm, respectively), a medium-sized group (24–42 cm and 28–60 cm, respectively) and a large-sized group (>40–50 cm and 55–65 cm to 100–120 cm, respectively). Specimens of the small-sized group are primarily found in the equatorial areas. Individuals of the medium-sized group are found throughout the whole species range (except in the most high-latitude parts); while those of the large-sized group occur primarily at the northern and southern peripheries of the range (usually poleward of latitudes 10–15°). However, large squids sometimes are found in equator-ward-flowing nearshore cold currents, particularly in the coastal branch of the Humboldt Current System (Nigmatullin et al. 2001).

In this paper we examine the changes in the size-at-maturity of *D. gigas* adult females off the Peruvian coast during 1989–2004. In particular we test the hypothesis that sea surface temperature controls the size-at-maturity in *D. gigas*.

### 1.3 - Methods and data

*D. gigas* biological data (mantle length, sex, maturity) were collected in Peruvian waters (i) during research cruises performed by the Peruvian Institute of the Sea/Instituto del Mar del Perú (IMARPE – <http://www.imarpe.gob.pe>) and (ii) from the artisanal and industrial fisheries from 1989 to 2004. For the industrial fishery, an observer aboard each vessel collected biological and fishery data. For the artisanal fishery, biological data were obtained from the landings. Mantle length (ML) was measured to the nearest mm. Sexual maturity was assessed with the macroscopic scale proposed by Nesis (1970) and modified by Tafur & Rabí (1997). This scale defines four stages for females: I (immature), II (maturation), III (mature), and IV (spawned). In this paper, mature individuals were those assigned to stages III or IV. The mantle length (ML) of adult females was used to identify the three different length-at-maturity population groups described by Nigmatullin et al. (2001). Length-at-maturity was determined during the main spawning season from October to January (Tafur et al. 2001).

We used monthly sea surface temperature anomalies (SSTA) as a proxy of environmental conditions for the period 1989 to 2004 in the region Niño 1+2 (0–10°S, 80°–90°W) and two coastal areas in Peru (Paita: 05°04.9’S 81°06.7’W and Callao: 12°03.3’S 77°08.8’W, Figure IV-1). SSTA for the region Niño 1+2 were obtained from the web page of NOAA (<http://www.cdc.ncep.noaa.gov/data/indices/ssta.indices>), while SSTA from Peruvian coastal areas were obtained from IMARPE.



*Figure IV-1 Areas where sea surface temperature anomalies were obtained: El Niño 1+2-area (0°–10°S 80°–90°W) indicated by square and three Peruvian ports: Paita, Callao and Ilo.*

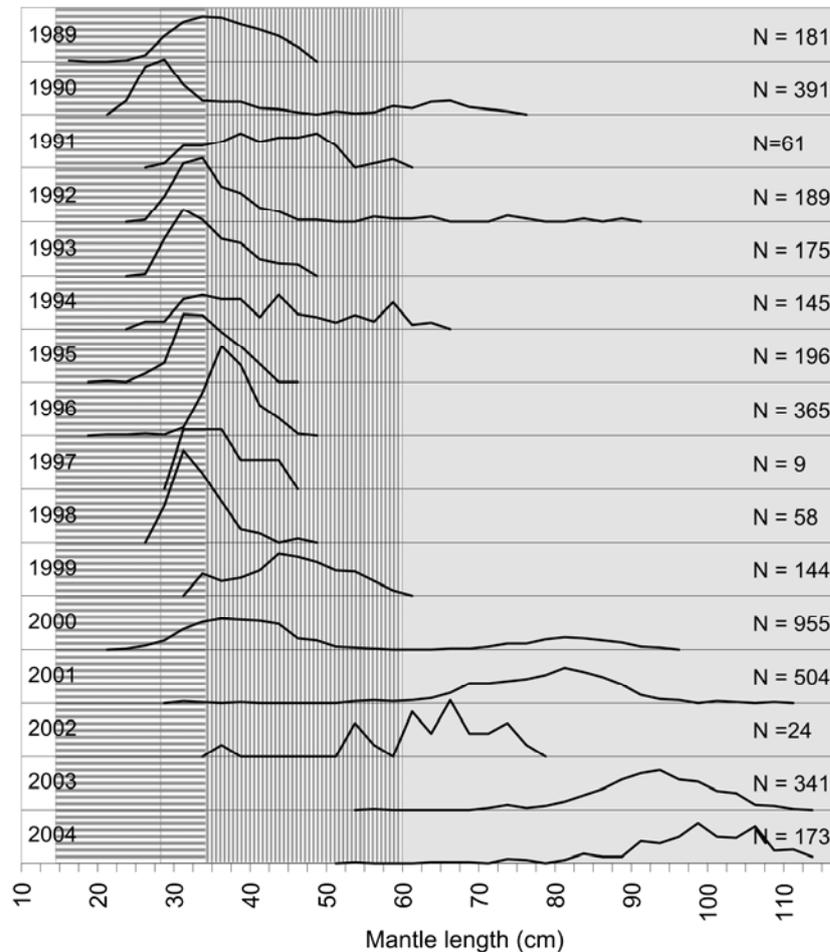
We used classification and regression trees (CART, Brieman et al. 1984) to assess the relative importance of year, month and the different time series of SSTA to length-at-maturity. In CART the dependent variable is modelled as a function of covariates. CART divides the data set through a sequence (tree) of binary splits on the values of one of the covariates at a time such that the overall variance in the dependent variable is minimized at each split. The resulting CART tree is usually simplified (‘pruned’) for the clarity of explanation.

## 1.4 - Results

### Female length-at-maturity

During the study period ML of mature females ranged between 14 and 113 cm (Figure IV-2 and Figure IV-3). According to the length-at-maturity population groups described by Nigmatullin et al. (2001), from 1989 to 1999 a majority of females reached maturity at medium-sizes (28–60 cm). During 2000 medium and large groups of size-at-maturity

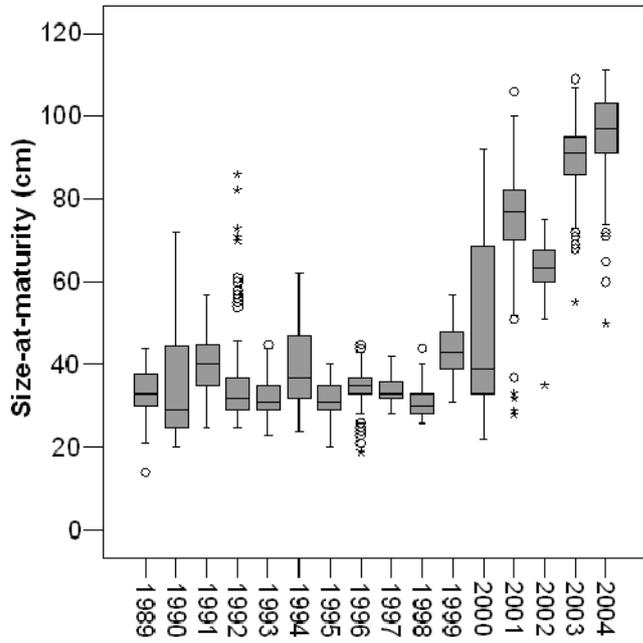
were observed, but from 2001 on, the large-sized maturing groups were dominating Peruvian waters. Large squid also occurred during 1990 and 1992 but in a lesser frequency. The small-sized maturing group was only abundant in 1990.



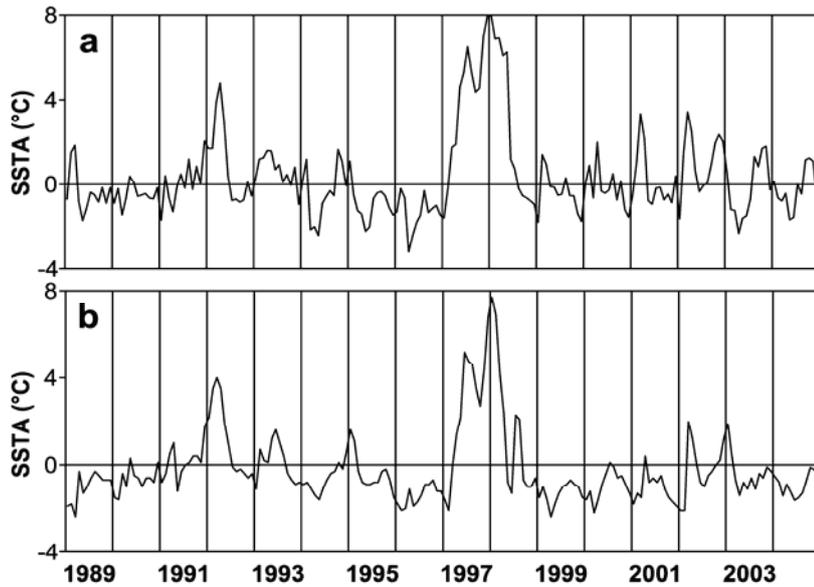
**Figure IV-2 Annual size structure of mature female of *Dosidicus gigas* in Peruvian waters from 1989 to 2004. Ranges of size-at-maturity according to Nigmatullin *et al.* (2001) are indicated by different areas, small sized (horizontal lines), medium sized (vertical lines) and large sized (grey).**

The time series of SST anomalies (Figure IV-4 shows the time series of SSTA of Paita and Callao) illustrates the strong El Niño (EN) of 1997–1998 (Wolter & Timlin 1998; Morón 2000), with positive anomalies ( $>+1^{\circ}\text{C}$ ) from March 1997 to July 1998 (16 months). Positive SST anomalies also occurred from February to June of 1992, corresponding to moderate EN conditions (Morón 2000). Cool periods were observed, principally during the 1996 La Niña (LN, Morón 2000), when negative SST anomalies ( $<-1^{\circ}\text{C}$ ) occurred from April to December. Negative anomalies were also predominant in Peruvian

coastal waters and in the Niño 1+2 region after the 1997–1998 EN. In the northern coastal waters near Paíta, short periods of positive anomalies occurred from 2001 to 2004 (Figure IV-4).



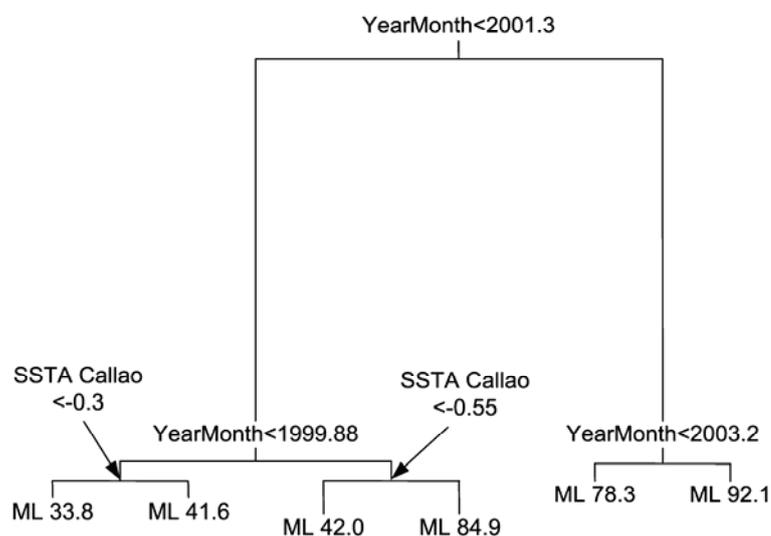
*Figure IV-3 Annual variation of length-at-maturity (ML) of females in Peruvian waters. Each box shows the median, quartiles, smallest and largest not atypical values. Circles and asterisks indicate extreme and atypical values, respectively.*



*Figure IV-4 Monthly time series of SSTA (sea surface temperature anomalies) in two coastal areas in Peru. (a) Paíta and (b) Callao, from 1989 to 2004.*

### CART analysis

CART results (Figure IV-5) indicate that the parameter having by far the strongest effect on the length-at-maturity is year. During 2000 the population transitioned from small to large squid (Figure IV-2 and Figure IV-3). Before January 2001, mature females were medium sized (mean ML 37.4 cm) while after this, the mean mantle length was much larger (mean ML 86.1 cm). In CART the year 1999 and SSTA off Callao had the second most important effects, but these results are much weaker, inconsistent, and not readily interpretable. There was thus no clear link between the length-at-maturity and SSTA.

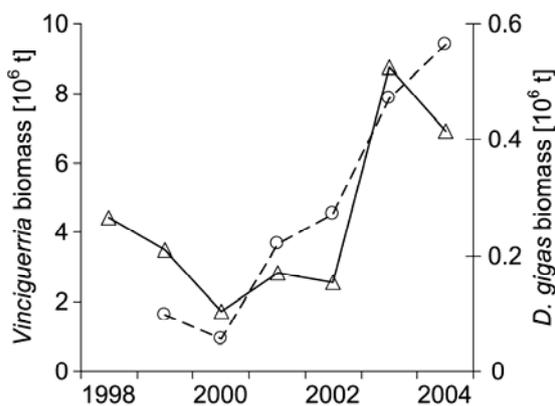


*Figure IV-5 Result of the classification and regression tree assessing the relative importance of year, month and the different time series of SSTA to length-at-maturity. The tree is split off on the values of one of the covariate at a time such that the overall variance in the dependent variable is minimized at each split.*

### 1.5 - Discussion

The results reported in this paper show a dramatic increase in the length of mature female *D. gigas* in Peruvian waters over the period 1989–2004. From 1989 to 1999 the mean length-at-maturity of females (37.4 cm) fell within the medium-sized group of Nigmatullin et al. (2001). From 2001 on, mean length (85.9 cm) fell within Nigmatullin et al's large-sized group. We did not observe the small-sized group reported by Nigmatullin et al. (2001) except in 1990 (Figure IV-2). The dominance of the medium-sized group during the 1990s agrees with Nigmatullin et al. (2001) who found this group in the entire

distribution area of the jumbo squid except in the most extreme parts of its distribution. We found medium-sized mature squids over a wide range of environmental and temperature conditions, for instance during the El Niño 1992 and 1997–1998 and the La Niña 1996 and 1999 (see Figure IV-4 for SSTA). We could not evidence any direct relationships between size-at-maturity and SST, at least at the scale of our study. In the case of the Peruvian waters characterized by their high productivity, in particular in terms of fish (Bakun & Weeks 2008), other factors such as food availability (Mangold 1987) could be determined. The increase in length-at-maturity and abundance from 2000 on (Figure IV-6) is concomitant with the significant changes for the spatial distribution of anchovy and sardine and the beginning of the ‘full anchovy era’ in Peruvian waters after 1999 (Gutierrez et al. 2007). From 2000 to 2004 the Peruvian upwelling system was characterized by (i) increased areal extent of the upwelled cold coastal waters (Swartzman et al. 2008), (ii) high coastal productivity and recovery of the annual primary production ( $>0.2 \text{ Gt C year}^{-1}$ ) after the 1997–98 El Niño (Carr 2002), (iii) increased in secondary production (Ayón et al. 2008), and (iv) an increased population of one of the most important preys of *D. gigas* (Figure IV-6), lanternfish of the genus *Vinciguerria* (Shchetinnikov 1989, Markaida & Sosa-Nishizaki 2003). The parallel lanternfish and jumbo squid population trajectories may suggest that an increase in prey availability caused the increase in the length-at-maturity of *D. gigas* off Peru.



**Figure IV-6** Annual mean biomass of *D. gigas* and *Vinciguerria lucetia* estimates by acoustic methods during research cruises in Peruvian waters (Imarpe unpublished data). Circles: *Dosidicus gigas*; triangles: *Vinciguerria*.

Fisheries can also affect population size structures, and for jumbo squid a purely industrial fishery slowly changed to a mixed industrial/artisanal fishery from 2000 on (Taipe et al. 2001, IMARPE unpublished data). But fishing typically produces decrease in size at maturity, in opposition to the abrupt size increase observed in 2000. Additionally, similar large mature groups were also observed off Chile from 2000 on (Zúñiga 2006), off Mex-

ico from 1995–2004 (excepting 1998 to 1999, Markaida 2006, Bazzino et al. 2007), in Oregon in 1997 (Percy 2002), and off British Columbia in 2004 (Cosgrove & Sendall, <http://www.thecephalopodpage.org/Dosidicusgigas.php>). In these widely distributed regions the history of the fisheries on *D. gigas* is completely different from that off Peru, suggesting a basin-scale environmental forcing.

***Acknowledgements.*** The authors thank the anonymous referees who greatly improved the manuscript through their criticism. A special thank to A. Bertrand who helped us with statistical analysis.

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## **2 - Reproductive biology of jumbo squid (*Dosidicus gigas*) in relation to environmental variability of the northern Humboldt Current System**

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**Manuscript submitted to Marine Ecology Progress Series**

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Tafur R, Keyl F, Argüelles J (subm) Reproductive biology of jumbo squid (*Dosidicus gigas*) in relation to environmental variability of the northern Humboldt Current System. Mar Ecol Prog Ser

## 2.1 - Abstract

Jumbo squid is a monocyclic ommastrephid squid and an important component of its ecosystems in the Eastern Pacific Ocean. In the past it has been found to show variable reproductive characteristics; among these were three spatially separated groups of size-at-maturity. Here biological data from the industrial fisheries of the Peruvian Humboldt Current System (HCS) from 1991 to 2007 were analyzed. Results showed that changes in reproduction patterns allow jumbo squid to cope with productivity changes in its environment. Three general reproduction-related features to adjust to changes have been identified: (1) variable size-at-maturity, (2) temporal decoupling of male and female formation of reproductive tissue in order to temporally distribute the required energy and (3) changing sex-ratios. Smaller sizes-at-maturity are found in warmer, less productive waters masses while specimen maturing at larger sizes are related to cool, productive water masses. Females mature at the end of their life which is leading to a j-shaped increase of maturity when plotted vs. mantle length while males mature at a medium size which results in a s-shaped form of maturation. The three groups of size-at-maturity proposed in earlier studies may not actually exist and could only be an observation artifact of a continuous change of size-at-maturity between two extremes.

## 2.2 - Introduction

The jumbo squid, *Dosidicus gigas* (d'Orbigny 1835) is found in pelagic waters off the coasts of the highly variable Eastern Pacific Ocean (EPO) in both hemispheres. This ommastrephid cephalopod has access to a wide range of prey sizes and trophic levels during its short life (Nigmatullin et al. 2001, Markaida et al. 2006a) that together with its abundance makes it a key predator in its ecosystem (Field et al 2007, Rosas-Luis et al. 2008). As *D. gigas* is a monocyclic species – i.e. it dies after its first reproduction cycle (Rocha et al. 2001) – its final size is related to its size-at-(first)-maturity. During its reproductive cycle female jumbo squid shows spawning with 10 to 14 distinct spawning batches. With 32 million eggs and more it has the highest fecundity of all cephalopods and fecundity is directly related to size (Nigmatullin & Markaida 2008). Females, although immature, can store male sperm in buccal spermathecae after copulation (Nesis 1983). This pattern is found in many cephalopods and increases reproductive flexibility and helps to secure population survival in variable environmental conditions (Boyle & Rodhouse 2005). With very few short-time exceptions (Markaida & Sosa-Nishizaki 2001) the sex-ratio of jumbo

squid has been found to be in favor of females, ranging from 1:1 to a ratio as high as 24:1 (Table IV-1).

Around the turn of the millennium changes in distribution have been found for different stocks of *D. gigas* (Zeidberg & Robison 2007, Keyl et al. 2008), reproductive biology (Markaida et al. 2006b in Mexican waters, Argüelles et al. 2008 in the Peruvian exclusive economic zone (EEZ)) as well as population structure in general (Bazzino et al. 2007). Analyzing size-at-maturity of females of the Peruvian EEZ, a transition period lasting roughly from 1999 to 2000 was identified that separates a period of small mature females in the 1990s from the period with large ones in the 2000s (Argüelles et al. 2008). At the same time landings of jumbo squid have increased strongly (IMARPE, unpublished data and FAO, <ftp://ftp.fao.org/FI/STAT/summary/a1e.pdf>). Temporal variation in size-at-maturity has also been observed in the northern hemisphere although in a different form. There, generally jumbo squid matured at large sizes at least since the late 1980s and size-at-maturity dropped to sizes similar to those found in Peru during the early 1990s only during the EN-event 1997/98 (Markaida et al. 2006b, Bazzino et al. 2007). However, before 1990 small specimens were also reported from Mexican waters (Table IV-1).

The northern Humboldt Current System (HCS) shows high variability of abiotic and associated biotic conditions. Water temperature, salinity and ecosystem productivity is coupled to water masses that change their extensions according to global climate conditions and events like e.g. El Niño (EN) and La Niña (LN) but also to larger-scale regime shifts (Morón & Sarmiento 1999, Morón 2000, Tomczak & Godfrey 2005). Cool water masses are generally assumed to be more productive than warmer ones (e.g. Ayón et al 2008a, b). Observed changes in size-at-maturity of *D. gigas* have been proposed to be a phenotypic response to changes in its physical and biotic environment (Nesis 1970, 1983, Keyl et al. 2008) or of genetic origin (Nesis 1970, 1983). The work of Nesis is based on partially unpublished work of the Russian scientific cruises from the 1960s to the 1980s. It proposes three different groups of size-at-maturity that are thought to be found in different zones of the distribution area: the small group in the tropical region, the medium-sized group throughout the whole distribution area and the large group in the distribution limits in both hemispheres (Nesis 1970, Nesis 1983, Nigmatullin et al 2001).

**Table IV-1: Reproduction parameters of *D. gigas*; GoC: Gulf of California, HCS: Humboldt Current System; EEZ: Exclusive Economic Zone; BC: Baja California Peninsula.**

ML [mm]	Fem:Male	Year(s)	Location	Source	Comments
*) ♀ 200 *) 200...350	1.5 ... 5.2:1	-	GoC Pacific off BC	<sup>3,5)</sup> Sato 1975, 1976	5 (sub-) populations acc.to oceanogr. cond.
<sup>4)</sup> ♀ 400...600	-	-	East of Peru- Chile trench	<sup>5)</sup> Shevtsov 1970	
♀ >400 ♂ <250	mean 2:1	-	HCS	Nesis 1970	size dependent fem:male-ratio
♀ 400...600 ♀ <270 ♂ <180	-	div.	“mile 201” HCS off Nicaragua	Nesis 1983	review
♀ 350...400 ♂ 180...250	-	1980	GoC, Pacific off BC	Erhardt et al. 1983, <sup>3)</sup> 1982, <sup>3)</sup> 1986	repro. cycle changes acc. to oceanogr. cond.
♀ 300 ♀ 260...330	1.5...3:1 1.82:1	1981	GoC Pac. off BC	<sup>3)</sup> Ramírez & Klett 1985	
*) ♀ 150...470 *) ♂ 170...450	7.34:1	11 & 12/1989	Peru	Rubio & Salazar 1992	
*) 500...700	1...24:1, mean 6:1	1989/90	GoC	<sup>3)</sup> Morán-Angulo 1990	
*) ♀ 660...800 *) ♂ 550...730	7.62:1	3/1990	GoC	Sánchez 2003, <sup>3)</sup> 1996	65% mature 85% mature
*) 300...750	2.6:1	1991	GoC	<sup>3)</sup> Guerrero- Escobedo et al. 1992	
♀ 420 ♂ 510	3.3...14.3:1 mean 5:1	-	GoC	Hernández-Herrera et al. 1996	
-	~2...8:1 mean 2.85:1	-	Peru EEZ	Tafur et al. 2001	
-	9:1 3:1	W 93 SPR 93	central Chile	Chong et al.2005	
<sup>1)</sup> ♀ 890 *) ♀ 470, ♂ 471	12.4:1 2.5:1	W 93 SPR 93	central Chile	González & Chong 2006	total 3.8:1
<sup>6)</sup> ♀ 420, 760 <sup>6)</sup> ♂ 600, 680	1.1...4.9:1 mean 2.3:1	1995/96 1996 1996/97	Guaymas Sta. Rosalia Guaymas	Markaida & Sosa- Nishizaki 2001	
♀ 310...458 ♂ 322...429	2.3:1 1.21	5/1999 9/1999	GoC Pacific of BC	Markaida 2006b	total 2.21
♀ 327 ♂ 228	2.52:1	2001	west of Peruvian EEZ	Ye & Chen 2007	
♀ 740	4:1	2001/02	GoC	Díaz-Uribe et al. 2006	
♀ 720	1:3...9:1	2001/02	Sta. Rosalía, GoC	Martínez-Aguilar et al. 2004	
<sup>2)</sup> ♀ >710 <sup>2)</sup> ♂ >660	min. 1.3:1 max. 4.5:1	S 03/04 W 03	central-south Chile	Ibáñez & Cubillos 2007	coastal oceanic
<sup>6)</sup> ♀ 770, ♂ 570 <sup>6)</sup> ♀ 690, ♂ 590	1.45:1 1.72:1	2003 2004	Sta. Rosalía, GoC	Bazzino et al. 2007	
<sup>1)</sup> ♀ 763, ♂ 796	1.25:1	W 05	centr.-south Ch.	Ulloa et al. 2006	by-catch of hake trawl fishery

\*) total sampled mode; <sup>1)</sup> mean of mode of mature specimens; <sup>2)</sup> mode of mature specimens; <sup>3)</sup> cited in Markaida & Sosa-Nishizaki 2001; <sup>4)</sup> only immature; <sup>5)</sup> cited in Nesis (1983); <sup>6)</sup> ML<sub>50%</sub>

Shifts in reproductive biology like size-at-maturity, female:male-ratio and rate of mated females (Table IV-1) according to oceanographic conditions have been mentioned but not specified for *D. gigas* of the Gulf of California and the Northern Mexican Pacific in the 1970s and 1980s (Sato 1975, 1976, Erhardt et al. 1982, 1983, 1986; all cited in Markaida & Sosa-Nishizaki 2001).

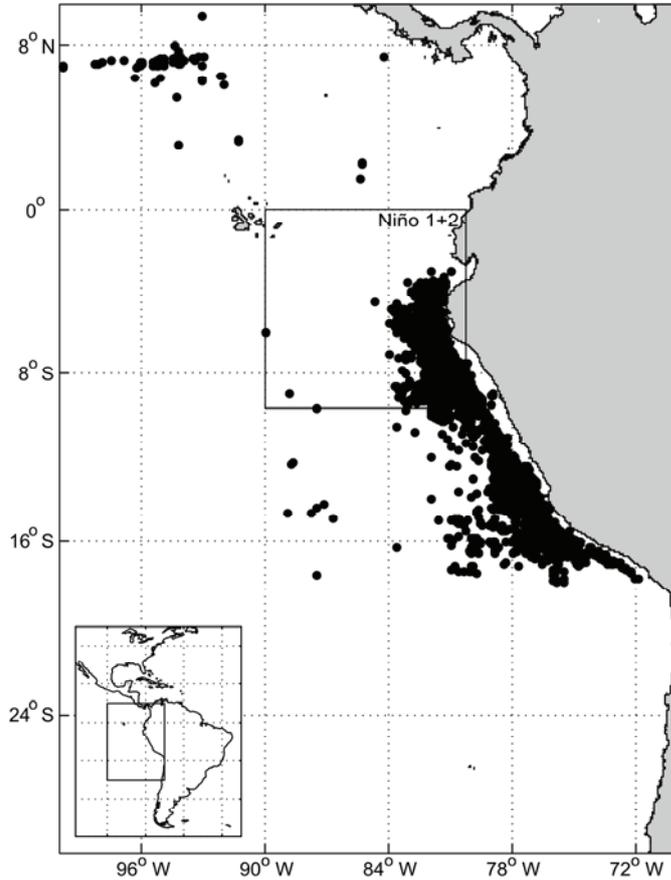
This work aims to identify and understand changes in the reproduction characteristics of *D. gigas* in relation to changing environmental conditions. It analyses data of nearly two decades that include the strong LN of 1996 and the strong EN of 1997/1998 as well as the shift from warm to cool conditions in 2000. The energetic implications of size changes and other reproduction related strategies are discussed. A simple model for energy allocation is put forward to explain the relation between size-at-maturity and cool and warm periods. The present work continues and amplifies the study of Tafur et al. (2001).

### **2.3 - Data and methods**

Study area is the Peruvian exclusive economic zone (EEZ), the northern part of the Humboldt Current System (HCS) where the coastal and the oceanic branch of the north and west flowing Humboldt Current are counteracting the oppositely pushing equatorial undercurrent (Tomczak & Godfrey 2005). The year-round stable wind-driven upwelling cells along the coast of Peru make its ecosystem one of the most productive in the world (Ayón et al. 2008b).

Data used in this study were collected by onboard technical observers on behalf of the Instituto del Mar del Perú (Peruvian Institute of the Sea – IMARPE) during the operations of the international jigging fleet in the Peruvian EEZ from 1991 to 2007 (Figure IV-7). The biological data base with more than 145,000 cases contains information on individual mantle length (ML), sex and reproduction related variables. During each fishing operation 10 females and 10 males were sampled from the catch. All length measurements (mantle lengths, gonadal lengths, nidamental gland lengths) were taken to the closest millimetre or half centimetre. Not all measurements have been taken or are available in all cases. Individual maturity was determined by a simple visual system as described in Tafur et al. (2001). It consists of four stages discriminated by size and color of the gonads where stage I contains the immature specimen, stage II the maturing ones and stage III the ma-

ture individual. Stage IV exists in case of the females only and contains the spawned specimens.



*Figure IV-7 Study area with sample locations; samples taken in the northern hemisphere were taken from August to December 1996 (n = 1612); samples west of 85° were taken in June 2000 (n = 215) and April 2005 (n = 19); the square is the Niño 1+2 monitoring area.*

Two reproduction related sizes were used to assess the stage of maturity of the population: (1) size-at-first-maturity or, in case of the monocyclic jumbo squid, simply size-at-maturity of the population is defined as the mean size of all mature individuals ( $ML_{\text{mean}}$ ), and (2) the size of massive maturity ( $ML_{50\%}$ ) that is defined as the ML where 50% of all individuals are mature (stage III and IV). Both were calculated by biological semester for females and males separately. Austral winters consist of the months April to September and austral summers of the months from October to March of the following year. A simple additive model assuming one to three Gaussian cohorts was adjusted to the semestral length-frequency distributions (with length classes of 30 mm) to test if the population distribution was homogenous or consisted of separated groups.  $ML_{50\%}$  was calculated by adjusting the sigmoidal model

$$\%mature = \frac{1}{1 + e^{-(a+b \cdot ML)}}$$

to the relative number of mature individuals (stages III and IV) in each 30 mm-size class as described by Tafur et al. (2001);  $\%mature$  is the relative frequency of mature individual in each length class  $ML$  and  $a$  and  $b$  are the parameters that describe the function.  $ML_{50\%}$  then was estimated as:

$$ML_{50\%} = -\frac{a}{b}$$

To be able to compare the semestral reproduction related series to SST the Niño 1+2 SST-anomalies series were transformed from its original monthly time increment to a semestral one by filtering the original series with 6-point running mean and using the values of the 4th and the 10th month of each year.

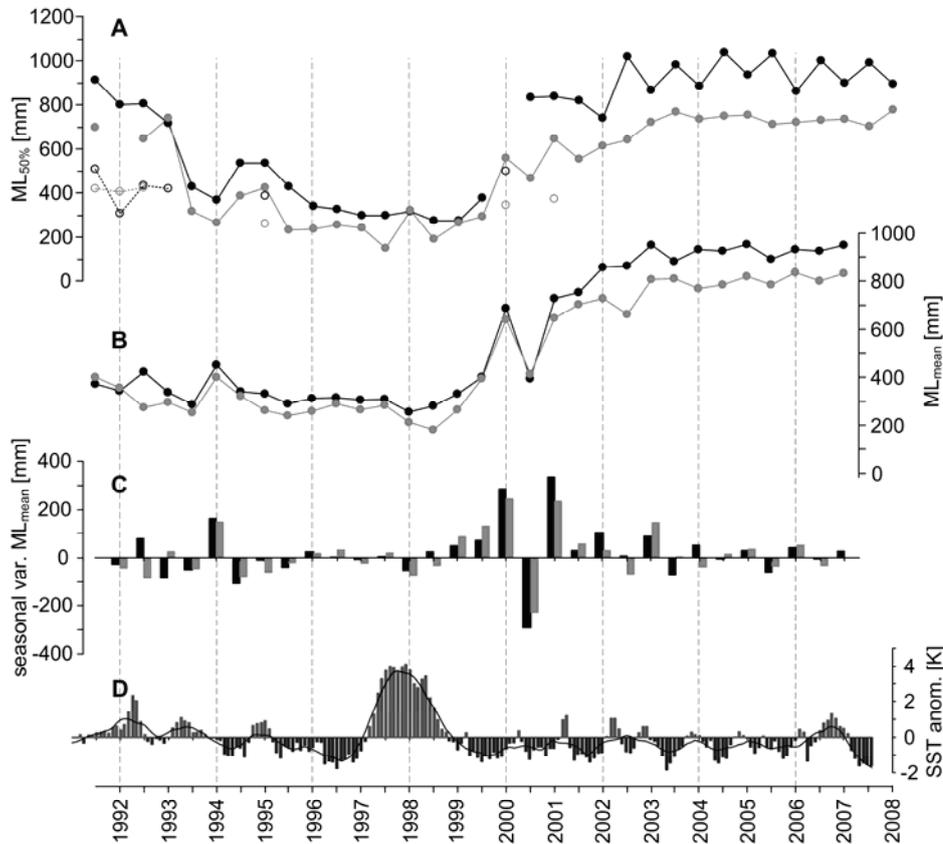
The length-based nidamental gland index as described by Tafur et al. (2001) that acts as a proximal indicator for individual maturity of females was used and extended to calculate a similar index for males using testicle length in relation to the mantle length. This maturity index (MI) was calculated for each individual as the percentage of nidamental gland length and testis length to ML for females and males respectively.

To identify reproduction and spawning periods the monthly mean MI for small and large individuals, the monthly proportions of mature individuals for females and males as well and percentage of copulated females were calculated. Females were considered as copulated if spermatophores were found in their buccal mass or if they had swollen spermathecae that contained rests of spermatophores. The monthly mean MI was calculated separately for small and large individuals to highlight the spawning peaks as it is assumed that in general the larger individuals of a population are those that are mature or will mature. The limit between the two groups was defined for each month by calculating the mean of all mature specimens (maturity stages III and IV for females and III in case of males) and subtracting one standard deviation to capture changes in size-at-maturity in different years.

The monthly sex-ratio (females:males) was calculated using data available of over 4.3 million individuals from 1996 to 2007.

## 2.4 - Results

Size-at-maturity ( $ML_{mean}$ ) and size of massive maturity ( $ML_{50\%}$ ) changed considerably in the study period (Figure 2A and B) during which total fisheries landings in the Peruvian EEZ increased rapidly from nearly zero in 1991 to its maximum of over 230,000 tons in 2006. In the early 1990s and in 2000 and 2001 more than one group each with characteristic  $ML_{50\%}$  were identified (open circles in Figure IV-8A). After a reduction in the period from 1993 to 1999,  $ML_{50\%}$  after 2000 reached similar values as that group with the higher

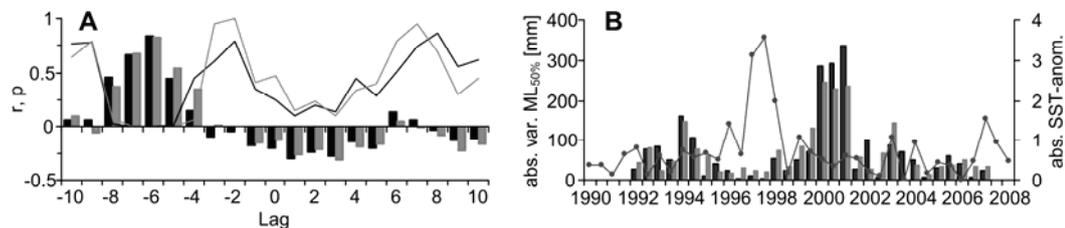


**Figure IV-8** Semestral variation in size of massive maturity ( $ML_{50\%}$ ) and size-at-maturity ( $ML_{mean}$ ) of female and male jumbo squid in the Peruvian EEZ in comparison to environmental variability; (A)  $ML_{50\%}$  for females (black) and males (grey); open circles: smaller group in years with more than one group of  $ML_{50\%}$ ; (B): absolute values of  $ML_{mean}$  for females (black) and males (grey); (C): variation of  $ML_{mean}$  between subsequent semesters for both sexes; (D): SST-anomalies of the Niño 1+2-box with 11 month centred running mean (line).

$ML_{50\%}$  in the years 1991 and 1992. The other group in these years that matured at smaller sizes were similar in size as those of the rest of the 1990s. After around 300 mm in the 1990s, during a transition period from winter 1999 to summer 2001  $ML_{mean}$  more than

doubled to above 800 mm and around 900 mm for males and females respectively. The inhomogeneous population structure found in some semesters for  $ML_{50\%}$  was not observed.

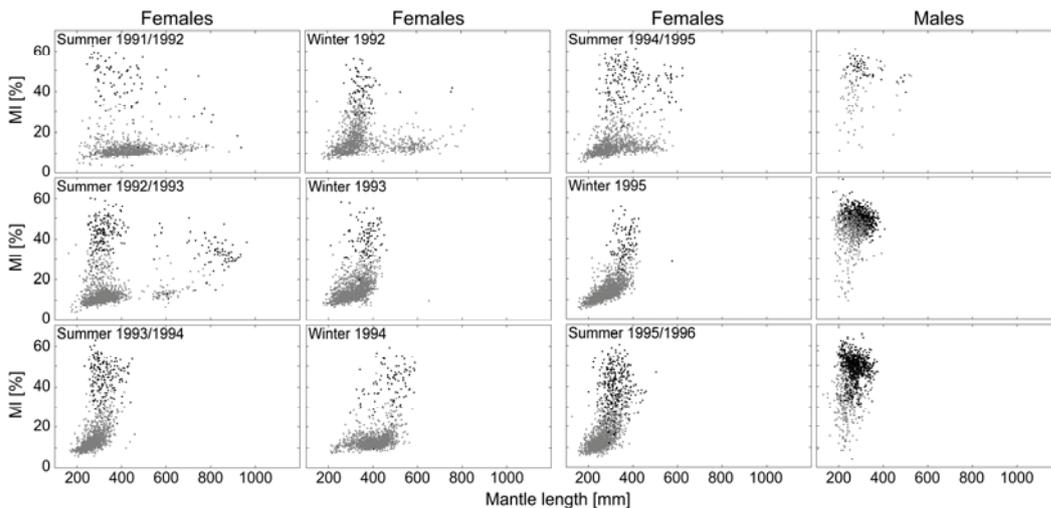
$ML_{50\%}$  and  $ML_{mean}$  of the females in nearly all semesters was above that of the males. Although the absolute difference between  $ML_{mean}$  of females and males increased in the 2000s, the differences between the sexes relative to body size decreased from 15.4% in the 1990s to 13.6% during the 2000s. During the transition period the differences between  $ML_{mean}$  of females and males were close to zero (Figure IV-8B).



**Figure IV-9** (A) cross-correlations between the absolute series shown in B; bars: correlation coefficient  $r$ ; lines:  $p$ -level; colours as before; (B) absolute series of seasonal variations of  $ML_{50\%}$  of females (black bars) and males (grey bars) and the mean seasonal SST-anomalies of the Niño 1+2-series (line with filled circles; every 6<sup>th</sup> point of a 6 pt. running mean of the original data to obtain a half-annual series relatable to the biological series) used for cross-correlations.

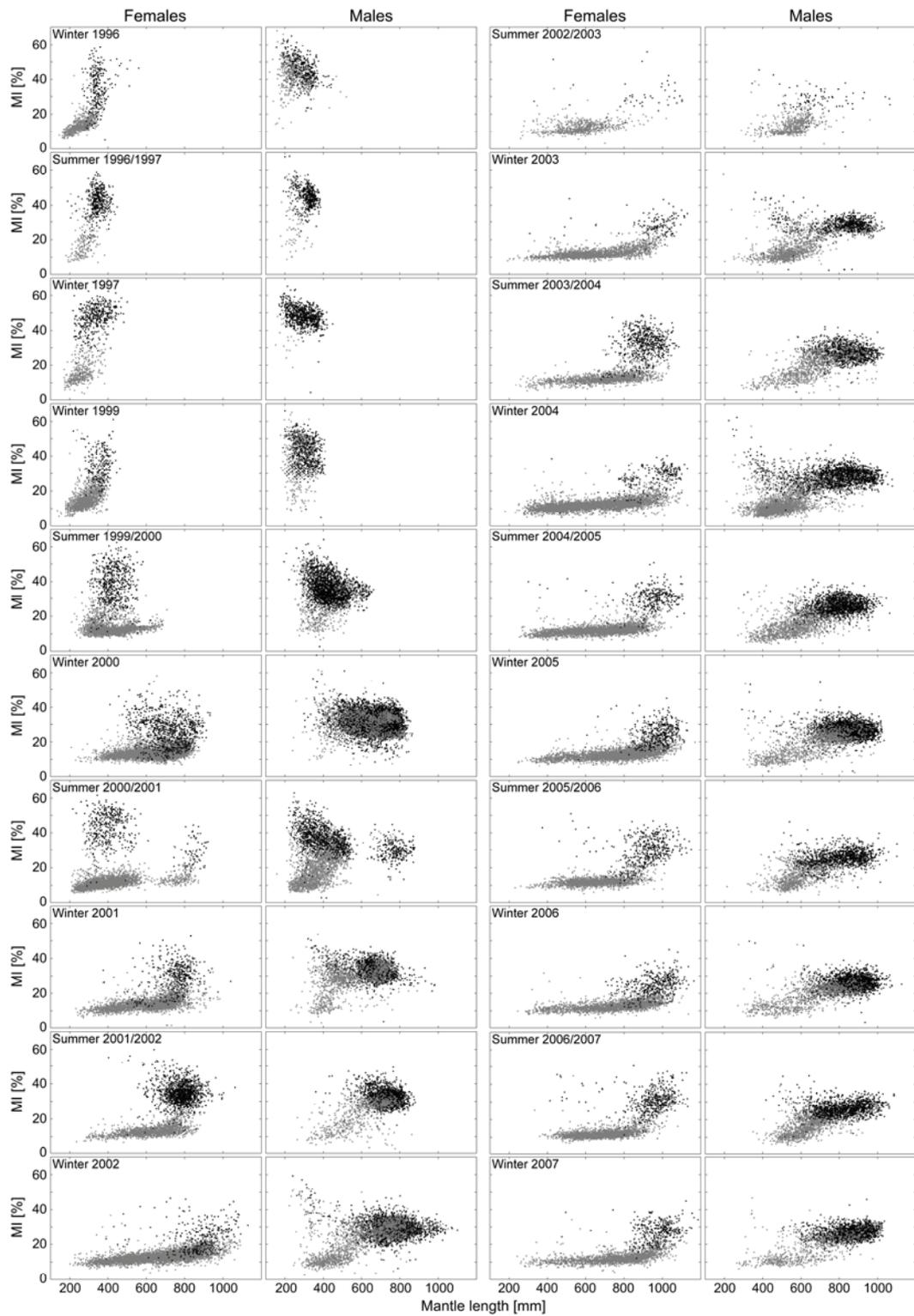
Highest inter-seasonal variation of  $ML_{mean}$ , both positive and negative (Figure IV-8C), can be observed after the EN-events of 1997/98 and, weaker, after that of the moderate EN of 1991/92. Direct cross-correlation analyses of the original  $ML_{mean}$ -series (Figure IV-8) and the intra-seasonal variation of size-at-maturity (Figure IV-8B) with the SST-anomalies of the Niño 1+2-box (Figure IV-8D) did not yield significant correlations between the series with any lag. However, when using absolute values of the semestral variation of  $ML_{mean}$  and the SST-anomalies series high significant correlations of up to 0.8 were found for lags from -4 to -7 and -4 to -6 for females and males, respectively (Figure IV-9). This translates to a delay of about 2 to 3 years of the biological response to environmental variability, i.e. the disturbance provoked by the EN-events is followed two to three years later by a change of size-at-maturity. For the  $ML_{50\%}$ -series that contains missing values that indicate delayed or even omitted massive maturity in such semesters, no clear relation to environmental series was found irrespective of lag.

The individual values of the maturity index (MI) plotted versus mantle length for each sex also show the difference between the 1990s and 2000s periods and the transition time from 1999 to 2001 (Figure IV-10 and Figure IV-11). The increase in size-at-maturity seems less clear as may be supposed from the  $ML_{\text{mean}}$ -series (Figure IV-8B). In 1991/1992, 1992/1993, 1994/1995 and from 2000 to 2002 more than one group of size-at-maturity can be observed similar to the results of the  $ML_{50\%}$  that in this years found more than one group (Figure IV-8A).

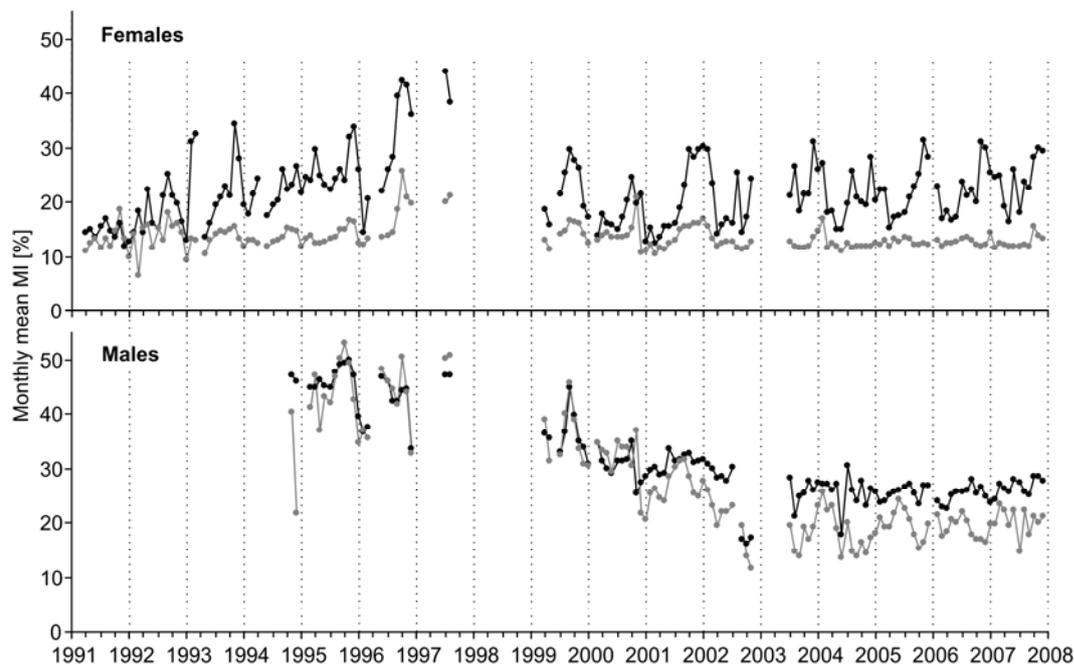


**Figure IV-10 Individual maturity index (MI) for female and males by semester 1991 to 1996; grey points: specimen classified as immature (stages I & II) by visual examination, black points: specimens classified as mature (stages III & IV); notice that from 1991 to 1994 no MI for males is available due to missing data.**

After 1999 the individuals started to become larger and distinct maturing processes for males and females can be noticed (Figure IV-11). While females grow continuously in body size without increasing their relative length of their nidamental glands until close to their maximum size, males start to mature at a size of about half their maximum size. After a combined growth of gonadal and somatic tissue (i.e. increase in testicle length and ML) further relative gonadal increase is stopped and only somatic growth takes place until the final body size. While females' gonado-somatic growth therefore can be seen as j-shaped leading to a soon death after maturing without further body growth, males gonado-somatic growth follows a s-shaped function that allows them to live on and grow in body size after completely maturing.



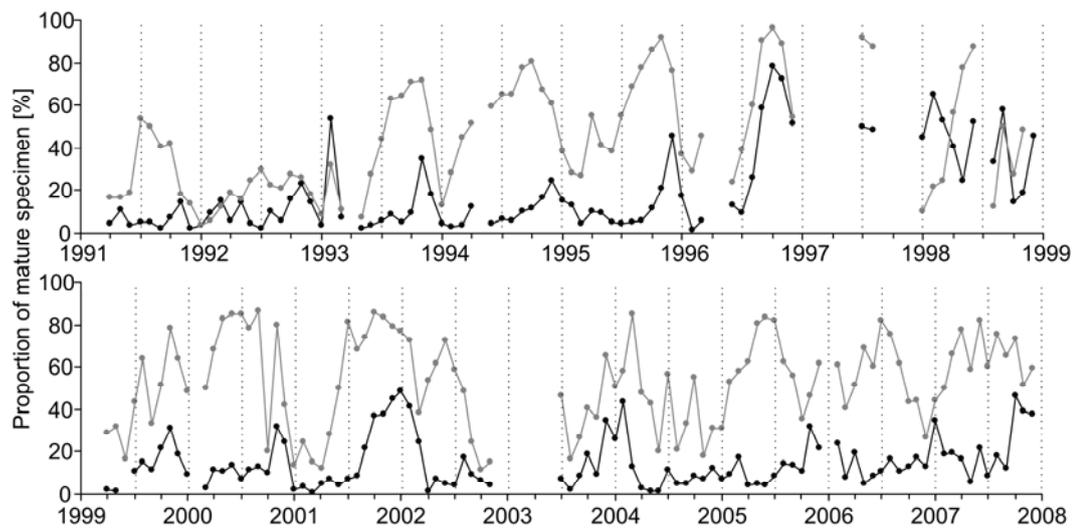
**Figure IV-11 maturity index (MI) for individual females and males by semester 1996 to 2007; grey and black dots as in Figure 4; note that no data is available for summer 1997/98 to summer 1998/1999.**



**Figure IV-12** Monthly mean values of the Maturity Index by sex for small (grey) and big (black) individuals.

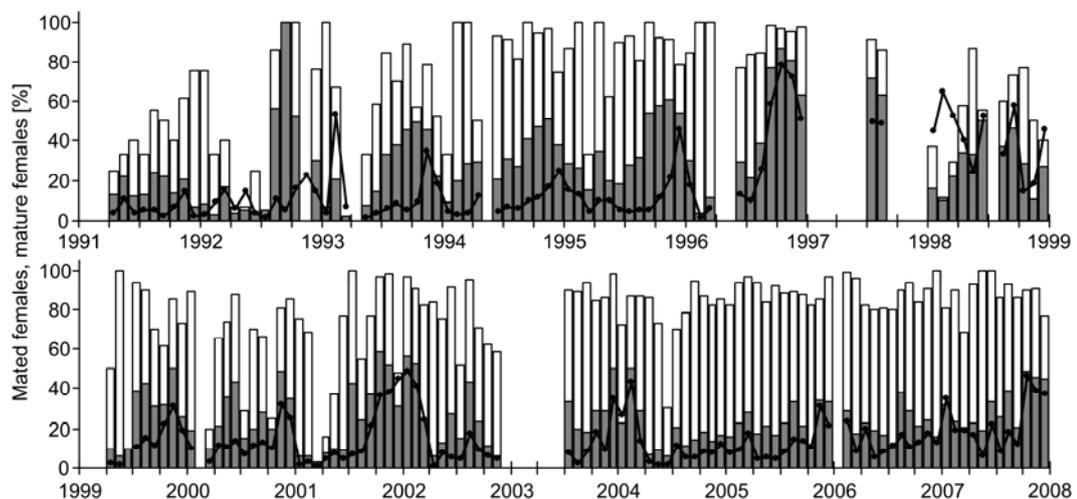
The monthly mean MI (Figure IV-12) not only show clear difference between small and large specimens but also between sexes. The MI of the small females is constant during the whole study period and the MI values of the large individuals show periodic or semi-periodic peaks and a continuous increase of mean MI in the early 1990s (Figure IV-12, upper panel). Main peaks occur around the end of most years. For males (Figure IV-12, lower panel), periodic peaks are found in both the large and the small specimens. However, the small ones show more marked and more regular peaks which can be expected in this form, as males show the s-shape gonado-somatic, or mid-life maturation, i.e. the large male specimens have already passed through maturation and from then on increase their gonad-size only relative to body size. The series of both groups of males in total show a constant decrease in mean MI until 2004 and a steady phase afterwards. A steady phase of the mean MI of the males during the early 1990s during which females increased their monthly mean MI can only be presumed as no data is available for males during the first years.

For the proportion of mature specimen in the population differences between sexes can be noticed (Figure IV-13). Mature males generally have a higher proportion in the male part of the population than the mature females have in the female part. Marked main reproduc-



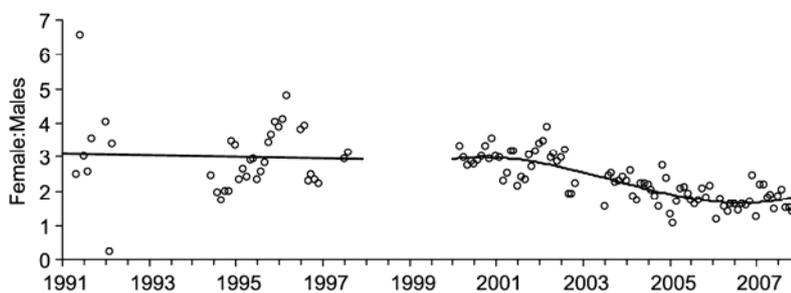
**Figure IV-13** Monthly percentages of mature individuals in the population; black: females; grey: males.

tion peaks occur at the end of the year (i.e. austral spring) until 2004 but become less clear and more frequent afterwards. Especially females after that year show an elevated maturity baseline with smaller peaks that less clearly show the annual periodicity observed in previous years. It is noticeable that the highest proportion of mature females was found in 1996 during the La Niña-event preceding the strong El Niño of 97/98. The reproductive peaks of males are generally wider than those of the females, resulting in a high constant overall percentage of mature males in the population broken up by short periods with lower percentages of mature males after the maturity peaks of the females.



**Figure IV-14** Monthly percentages of mated females among all females (grey bars) and among mature females (white bars); the dotted line indicates the percentage of mature females.

With the exception of some periods (1991 to 1993, 1998 and 2000/01), the fraction of mature females that have mated (white bars in Figure IV-14) exceeds 90% of mature part of the population in most month. The fraction of mated females in the entire population usually still reached between 20% and 50% (grey bars in Figure IV-14). Percentage of mated females usually increased or peaked with the onset of austral summer in October although this pattern was less marked after 2002. The percentage of mated females (grey bars in Figure IV-14) is related (exponential function,  $r^2 = 0.44$ ,  $p < 0.01$ ) to male maturity (see Figure IV-13).



**Figure IV-15: Monthly female to male ratio.**

Monthly sex-ratio (females:males) is highly variable, although not in the same three-partite pattern observed for  $ML_{50\%}$  and MI (Figure IV-15). In the 1990s and until around 2002 the monthly sex-ratio in average has been found to be around 3:1 in favor of females. After that year a slow decrease of the sex-ratio to around 2:1 has been observed. Sex-ratio between 6.55:1 and 0.24:1 were observed until 2002 while afterwards it changed to values between 3.86:1 and 1.09:1. Similar ratios and even higher ones have been reported before as has the high temporal variation of the ratio (see Table IV-1).

## 2.5 - Discussion

The results of the analysis of mean monthly MI and relative occurrence of mature individuals (Figure IV-12 to Figure IV-14) give strong evidence that main reproduction period of Peruvian jumbo squid is austral spring. This is consistent with the findings of previous work (Tafur & Rabí 1997, Tafur et al. 2001).

A strong shift of size-at-maturity of *D. gigas* in Peruvian waters was observed for both sexes similar to that reported before for females (Argüelles et al. 2008). It was taking place after the very strong climate events of the 1996 La Niña (LN) and the 1997 to 1998

El Niño (EN). After this “system reset” (Bakun & Broad 2003) a stable cool regime was especially noticeable in the study area (see Niño 1+2-box in Figure IV-7 and integrated SST-anomalies series of this area in Figure IV-8). Environmental conditions have been hypothesized to be important for changes in size-at-maturity of *D. gigas* (Keyl et al. 2008).

It is assumed that the onset of maturation in cephalopods is controlled mainly by temperature and nutrition availability. Higher temperatures and low food availability result in maturation at smaller sizes (Mangold 1987). From an energetic point of view the individuals maturing at small sizes are benefited over the larger ones as they need to put less energy in somatic and reproductive tissue before spawning. In the HCS temperature and nutrition availability are related: the warm water masses that dominate the system during warm periods are less productive than the cooler waters that prevail during cool periods (Ayón et al. 2008a, Ayón et al. 2008b, Swartzman et al. 2008). Additionally, the species dominance of the ecosystems of the HCS changes with the water masses (Chavez et al. 2003, Gutiérrez et al. 2007, Tam et al. 2008, Taylor et al. 2008). If it is understood that the Niño 1+2-series is the spatial integration of the SST of all water masses in this area it can easily be seen that negative anomalies correspond to the prevalence of cool waters while positive ones correspond to warmer waters. The temporally changing maturation patterns found here (Figure IV-8A and B) must then be related to different water masses and point out that the variable reproductive patterns of *D. gigas* via trophic links are the result of spatial variability of oceanographic factors. Specimens that mature at small sizes as were found in less productive warm water masses (Keyl et al. 2008).

The results of the cross-correlation between the absolute series of monthly variation of  $ML_{\text{mean}}$  and SST-anomalies indicate that changes in size-at-maturity are related to disturbance of the ecosystem (Figure IV-9). Longevity of jumbo squid in the past mostly has been assumed to be no more than 12 to 18 month (Masuda et al. 1998, Argüelles et al. 2001, Nigmatullin et al. 2001). The lag of two to three years between strong environmental variability (EV) and the biological response then translates to an inter-generational lag of the impact of changes in environmental conditions. A more recent work using data from the industrial fishery in the Peruvian EEZ found longevity to be highly variable and range from around 12 month up to 32 month only loosely related to terminal size of a cohort (Keyl et al. *subm. to MEPS.*). There, longevity of over two years was found for all

cohorts hatched in the period of the high environmental variability from 1996 to 1999. If it were true that longevity is actually higher as found before, then the observed lag of two to three years describes an intra-generational shift, i.e. a shift in environmental conditions directly and instantaneously affects life history traits or at least the maturity-related processes. This would also make the genetic origin of the changes as proposed by Nesis (1983) improbable. It has to be noted that the shifts found here occurred during a period of increasing fishing pressure and landings (IMARPE, unpublished data).

After both strong EN-events that occurred in the study period the effect of the “system reset” was noticed but after the 1997/98 EN the environment of the northern HCS entered into a cool phase (Figure IV-8D). This phase seems to have stabilized the change from small to large size-at-maturity that was triggered by the EN “reset”. The similar, but weaker changes in size-at-maturity of *D. gigas* that have been observed with a similar temporal lag after the weaker EN of 1992/93 supports this point of view. After the occurrence of a few cohorts of increased size-at-maturity without a lasting cool phase similar to that observed in the 2000s the size-at-maturity in the mid 1990s dropped again (Figure IV-9 and Keyl et al. subm.) to the small group that prevailed in the HCS since at least the end of the 1980s (Rubio & Salazar 1992). The fact that off Chile, in the cooler southern HCS until now only individuals maturing at large sizes have been found (González & Chong 2006, Ulloa et al. 2006, Ibáñez & Cubillos 2007), further indicates that size-at-maturity is coupled to water masses, i.e. temperature and nutrition conditions.

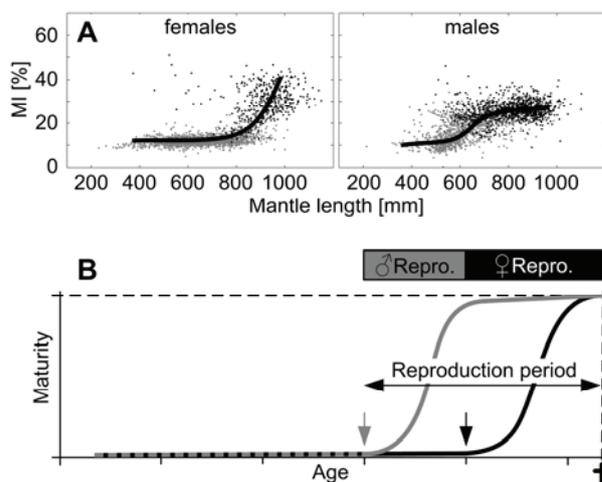
Temporal shifts in size-at-maturity also occurred in Mexican waters although only that after the 1996 to 1998 La Niña/El Niño-combination was described (Markaida 2006b). An earlier increase of size-at-maturity in the 1980s (see Table IV-1) has not been analyzed or explicitly mentioned but can be retrieved from a number of publications of the 1970s and 1980s. The exact year can not be determined as data is not available. Obviously during nearly the whole decade of the 1980s jumbo squid abundance was very low and fishery took place on the subsistence level only (Nevárez-Martínez et al. 2000, Markaida 2001). Changes in size-at-maturity or sub-population groups with different size-at-maturity have been reported for other cephalopods like e.g. the purpleback squid (*Sthenoteuthis oualaniensis*) in the Arabian Sea (Shulman et al. 2002) and the cuttlefish *Sepia officinalis* in the English Channel (Dunn 1999).

In the series of  $ML_{50\%}$  and  $ML_{mean}$  (Figure IV-8) as well as in the MI (Figure IV-10 and Figure IV-11) a gradual increase of size-at-maturity can be observed and it has to be doubted if three separated, but overlapping groups of size-at-maturity in spatially distinct areas of the EPO of Nesis (1983) and Nigmatullin et al. (2001) exist. The changes in size-at-maturity found now suggest a more continuous alteration of size-at-maturity between two extremes according to abiotic conditions that impact the productivity of the ecosystem. Results of the present work, as those of Markaida (2006b) for Mexican jumbo squid and Argüelles et al. (2008) for Peru, show temporal shifts in size-at-maturity instead of a spatial separation but in all three cases spatiality has not been addressed explicitly. To our knowledge, until now no data has been presented that clearly show the three groups of size-at-maturity of Nesis (1983) and Nigmatullin et al. (2001).

The overlay of mature and immature individuals (black and grey points) in one cloud found especially in some years (1995 and beginning of the 2000s) for males and less in case of females indicating the difficulty to visually assess maturity and the limitation of the used system. Another reason for this overlap of the different visually determined stages of maturity may be the multiple spawning scheme of jumbo squid (Rocha et al. 2001, Nigmatullin & Markaida 2008) as has been described more detailed by Staaf et al. (2008). They assume that the method for the classification of the maturity stages can not reproduce the repeated spawning batches as apparently after each spawning event little or no eggs remain in the oviduct and females although fully mature may be mistaken as maturing or immature. Until now it has not been described if and how multiple development of spermatophores occurs in males of *D. gigas* but it is possible that the system that is used here for males has a similar limitation in this sense. However, the here used length-based maturity index, the MI, may already reduce this problem. It has the advantage over the more commonly used weight-based indices as it classifies the maturity of the females (and males) relatively independent of oviduct fullness that changes due to the repeated spawning batches.

The semestral graphs of the individual MI after 2000 (Figure IV-11) display different somatic and gonadal growth patterns for the two sexes. They can be described as j-form in case of the females leading to soon death after reproduction and as s-shaped for the males that allows them to grow on after the onset of reproduction (Figure IV-11 and Figure IV-16A). As a result size-at-maturity of the two sexes is distinctly linked to terminal size:

while for females they are equal or nearly equal, for males this is not valid. Compared to their size-at-maturity their terminal size is clearly higher. Another, much more important effect of this different maturation processes is the temporal separation (Figure IV-13 and Figure IV-14) of the maturation of males and females, giving each sex the possibility to mature without elevated intra-specific competition for resources from the other sex (Figure IV-16B). Together with the fact that immature females can store spermatophores in their buccal membrane (Nigmatullin & Markaida 2008), it allows *D. gigas* to efficiently extend its reproductive period. Similar temporal decoupling of male and female maturation processes has been reported for octopus species in general (Forsythe 1993), *Illex illecebrosus* (O'Dor & Dawe 1998) and the *Sepia officinalis* population of the English Channel (Dunn 1999). The mating of immature females also explains the lag between increase in mating and maturation in females especially visible from 1993 to 1995 (line and grey bars respectively in Figure IV-14).



**Figure IV-16** Decoupled reproduction periods of females and males; (A) j- and s-shaped reproduction process of females and males respectively; example from summer 2005/06; grey/black points as in Figure IV-10 and Figure IV-11; (B) temporal representation of the distinct maturation processes of females (black) and males (grey).

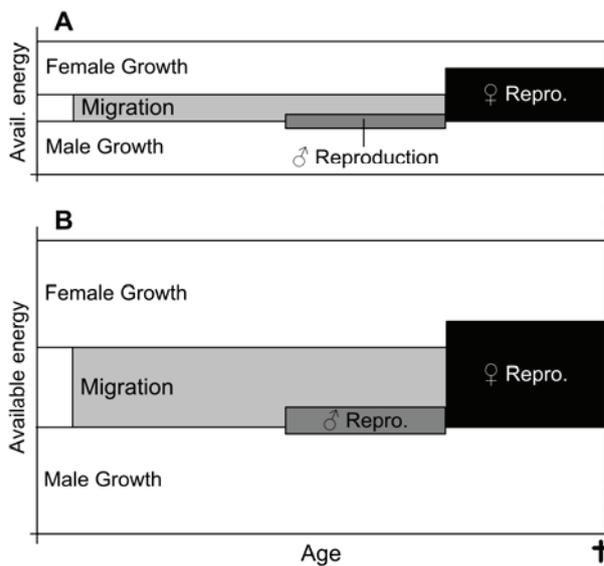
Gonadal growth needs energy and three principal sources or a combination of these may be assumed to provide this energy: (1) additional food intake, (2) less migration, i.e. less respiration and (3) reduced (or even zero or negative) somatic growth rates and maintenance. Cephalopods in general (Rodhouse & Nigmatullin 1996) and also *D. gigas* (Markaida & Sosa-Nishizaki 2003) are described as ferocious predators that due to its high somatic growth rates must have a high energy demand. Thus, it can be assumed that an increase of the already high feeding rate is difficult. Nevertheless, for the more demersal *Loligo gahi* it has been suggested that it may increase its ingestion rate during maturation to meet the higher energy demand (Ibáñez et al. 2005). For *D. gigas* is only known that feeding activity continues during the maturation and spawning phase without drop

off (Markaida et al. 2004, Nigmatullin & Markaida 2008). With respect to the second possible source of energy for gonadal tissue, migration, little is known in this respect for *D. gigas*. Normal and reduced migration has been described for cephalopods to gain energy for maturation without decreasing growth rates (Wells & Clarke 1996). Knowledge on the third potential source of energy, reduced somatic growth, similarly is limited but reduced somatic growth after the onset of gonad production was proposed for the myopsid squid *Alloteuthis subulata* (Rodhouse et al. 1998). In case of *D. gigas* no direct growth study exists on growth but it has been assumed that growth during maturation continues with the same rate as before (Markaida et al. 2004).

Highest oviduct weight found in this study was 2043 g for a female of 920 mm ML and 31.1 kg. Assuming 10 to 14 spawning batches (Nigmatullin & Markaida 2008) and complete evacuation of the oviduct during each batch (Staaf et al. 2008) the summed gonad weight of the largest females in the present dataset could total 28.6 kg or nearly the overall weight of this female. If assuming a very high conversion rate of 40% that is above that of Wells & Clarke (1996) for the ommastrephid *Illex illecebrosus* the formation of this tissue alone would require a food intake or its energetic equivalent of at least 71.52 kg or 600 to 715 g daily in the reproductive period of 100 to 120 days of Nigmatullin & Markaida (2008). A part of this amount must already be allocated to the primary formation of the oocytes during the immature part of life. Considering that a similar amount of energy is put additionally into the maturation of the nidamental glands during mature stage of life (Nigmatullin & Markaida 2008) we assume that the sum of 10 to 14 oviduct masses roughly represents the energy needed for reproduction during the actual spawning period. The approximately 5 kg of additional somatic tissue proposed to be build up during maturing and mature life stage (Markaida et al. 2004) would require another 12.4 kg of food intake assuming the same conversion efficiency. Potential fecundity and weight of the spawning batches is directly related to the size of the female (Nigmatullin & Markaida 2008) and it seems worth mentioning here that therefore smaller specimens need to invest relatively more but absolutely less ingested energy into reproduction than larger ones (Keyl et al. 2008).

If assumed that all three of the above mentioned sources of energy play a role to meet the costs of maturation and that male investment into reproduction are significantly lower than that of females, an energy allocation scheme as shown in Figure IV-17 could result.

This oversimplified and certainly questionable scheme explains larger sizes, higher absolute reproductive output and expanded energy available for migration during the cooler, nutrient rich periods. Parts of the energy needed for gonadal growth is reallocated from energy that before maturation is used for somatic growth. Such a reallocation of energy must result in temporally slowed down growth after the onset of maturation and, as males and females show distinct maturation processes, also should result in dissimilar growth curves of the two sexes. Results of an analysis of length-frequency data of Peruvian *D. gigas* show a reduction of growth rate of some of the larger cohorts short before their extinction (Keyl et al. *subm. to MEPS*).



*Figure IV-17 Scheme of hypothetical allocation of available energy during warm, less productive periods with smaller specimens (A) and cool, more productive periods with larger specimens (B).*

The monthly female:male-ratio and its variation (Figure IV-15) is in the range found by other studies in the whole distribution area (listed in Table IV-1). The shift to a lower female:male-ratio noticeable after 2001 is also interesting from an energetic point of view. After all, males do not directly contribute to reproduction; they are intra-specific competition for resources for the females, the actively reproducing part of the population. The reason that males exist is the very same why sexual reproduction in general exists: to foment genetic diversification allowing their species to adapt to changes in their environment. The mixed paternity of the progeny of one female reported for some cephalopods at least (Boyle & Rodhouse 2005) may be seen as a measure to reduce the amount of energy “lost” in the non-reproductive part of the population (i.e. the males) without losing too much opportunity to genetically diversify in every generation. The reduction of the sex-ratio (i.e. more males per females and a higher energy demand per progeny) found in the

2000s corresponds to the cool and more productive period in the Peruvian part of the HCS. However, no further support exists for this hypothesis and other explanations may equally be possible.

The present work analyzed maturation and reproduction of jumbo squid in relation to their size and large-scale environmental conditions. It remains unclear how these processes chronologically and spatially develop. We believe that jumbo squid with its extremely plastic reproduction patterns in relation to variability of its environment may act as a model organism to understand less extreme patterns of other marine and non-marine species that are more difficult to detect.

*Acknowledgements.* We thank all our colleagues at the IMARPE that kindly supported and advanced our work with their knowledge, experience and advice, especially those from the Marine Invertebrate Department and all on-board observers. F. K. in parts was financed by the EU-project CENSOR.

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### **3 - Interannual variability of population structure, age and growth of jumbo squid (*Dosidicus gigas*) in the Humboldt Current System**

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**Manuscript submitted to Marine Ecology Progress Series**

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Keyl F, Argüelles J, Tafur R (subm) Interannual variability of population structure, age and growth of *Dosidicus gigas* in the Peruvian EEZ. Mar Ecol Prog Ser

### 3.1 - Abstract

The ommastrephid jumbo squid is an important ecological and economic component in the highly variable Humboldt Current System (HCS). In the past a great range of values for growth rates, longevity, maximum size and annual cohort number has been found and genetic and phenotypic plasticity have been mentioned as possible sources of observed different maximum sizes. A length-frequency dataset with over 4.3 Mio cases taken from 1991 to 2007 in the jig fishery in Peruvian waters was used to analysis growth related parameters of 33 cohorts by a modal progression analysis (MPA) and relate results to environmental conditions. Calculated growth rates of different cohorts vary strongly (11 to 44 mm/mo) as do longevity (11.1 to 32.1 mo) and mean maximum size (273 to 1024 mm). Fast growing cohorts with medium longevity reaching large terminal sizes occurred during moderately cool periods while slow growing cohorts that are very long-lived reaching small terminal sizes were observed during extreme conditions of the ecosystem (i.e. El Niño and La Niña). No significant intra-annual difference of growth parameters was found and the number of cohorts per year varied between 0 and 6. Although the application of MPA to cephalopod populations has generally been rejected before, result here suggest that when using an approach that allows varying growth parameters and the correction of observation bias introduced by the specific fishing gear, MPA can be a suitable method for the evaluation of growth parameters.

### 3.2 - Introduction

The nerito-oceanic ommastrephid jumbo squid *Dosidicus gigas* is an important component of its ecosystems of the Eastern Pacific Ocean (EPO) (Field et al. 2007, Rosas-Luis et al. 2008). It supports a fishery that by landings in 2006 was the 12<sup>th</sup> most largest in the world (FAO, <ftp://ftp.fao.org/FI/STAT/summary/a1e.pdf>). In the Peruvian EEZ jumbo squid is fished by an international industrial fleet and two near-coast operating artisanal fleets in northern and southern Peru. All Peruvian fisheries on jumbo squid use jigs equal or similar to those used in a number of other squid fisheries world-wide (e.g. Hatanaka et al. 1985). The jigs are employed on a vertical line and consist of a varying number of hook crowns that are arranged one on top of each other. They are highly size-specific in dependency of jig length and hook size and show a nearly exact Gaussian distribution of the catchability. During fishery operations is selected to be most effective in the size range of the most abundant size group found in the water (J. Argüelles, unpublished data).

As most other cephalopods jumbo squid is a monocyclic species, i.e. it dies after its first reproductive season (Rocha et al. 2001) with 10 to 14 spawning batches (Nigmatullin & Markada 2008); its size-at-(first)-maturity as a consequence is related to its maximal size. An interesting aspect of the population structure of jumbo squid has first been reported by Nesis (1970). Three groups of size-at-maturity that result in different maximal sizes have been assumed to be restricted to different latitudes of its distribution area roughly following Bergmann's rule: a small group populates the tropical region, a middle-sized group is found in the complete distribution range and a big group occurs in poleward areas in both hemispheres. The three groups mature at dorsal mantle lengths (ML) of 130 to 340 mm, 240 to 600 mm and >400 to 1200 mm and females in average mature at larger size (Nigmatullin et al. 2001). More recent studies proposed and found a gradual change of size-at-maturity between two size extremes (Keyl et al. 2008, Tafur et al. *subm.*).

The origin of the groups has been proposed to be either a phenotypic (Nesis 1983, Keyl et al. 2008) or a genetic response (Nesis 1983) to environmental conditions. Temperature and/or food availability have been suggested as governing factors (Keyl et al. 2008). In the HCS these two factors are closely related to each other via water masses that are characterized mainly by temperature and productivity. Locations and extensions of water masses in the system change depending on basin-scale climate variability. During periods like El Niño (EN) warmer water masses that are less productive than cooler waters prevail in the northern, Peruvian part of the HCS whereas in other periods cooler water masses dominate (Ayón et al. 2008, Swartzman et al. 2008, Tam et al. 2008, Taylor et al. 2008). The occurrence of larger size-at-maturity of *D. gigas* that was found in Peruvian waters from around 2000 on (Argüelles et al. 2008) has been connected to the cooler water masses with higher availability of food; that of the smaller size-of-maturity to less productive warmer water masses (Keyl et al. 2008). Distinct from other squid species (e.g. *Illex argentinus*, Waluda et al. 2001, *Todarodes pacificus*, Kiyofuji et al. 2004) migration patterns e.g. between spawning and feeding areas are not known for *D. gigas* and at the moment seem unlikely as paralarvae have been found in the entire HCS (unpublished data J. Argüelles, IMARPE, Callao, Peru and C. Ibáñez, IEB, Santiago de Chile).

Based on the review of a number of publications, lifespan by Nigmatullin et al. (2001) was assumed to be one year for all three groups of size-at-maturity although the biggest specimens of the big group might reach two years. These findings would indicate differ-

ent growth rates for the different size groups and disagree with the finding of Argüelles et al. (2001) who found different life spans for the different groups. To clarify this discrepancy previous studies are reviewed here (Table IV-2). They either used modal progression analysis (MPA) based on length-frequency analysis (LFA) or the analysis of statolith rings to assess longevity and growth rate. The statolith rings counted are generally assumed to mark daily time increments. However, although daily increments have been confirmed for a number of cephalopod species, to our knowledge this assumption remains untested by ageing studies for *D. gigas*.

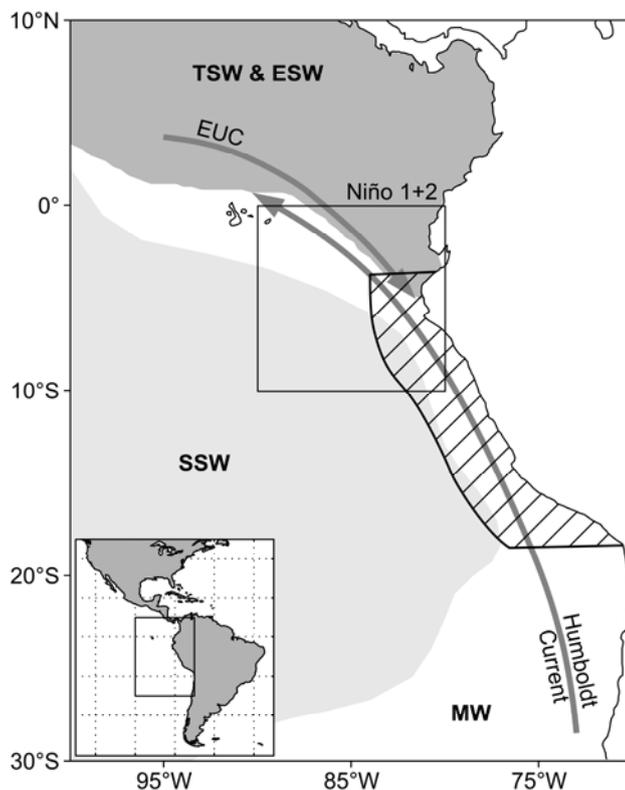
**Table IV-2: growth parameters of *D. gigas* from 1981 to 2004 in different areas of the EPO as obtained by MPA and statolith-analysis; GoC: Gulf of California, Mexico; EEZ: exclusive economic zone.**

Area	Sample date	Max. longevity/size	Growth rate [mm/yr]	Method	Reference
-	-	1 yr/200...350 mm 2 yr/300...500 mm 2...>4 yr?/ > 500 mm	200...330	MPA: assuming one cohort/yr	Nesis (1970)
GoC	-	2 yrs	700...750	MPA	Ehrhardt et al. (1983)
Outside EEZ Peru & Ecuador	3/81... 2/84	2 size groups	690...735	Statolith	<sup>1)</sup> Arkhipkin & Murzov (1986)
Off Peru	87...95	1 yr, 2 size groups	-	Statolith	Masuda et al (1998)
Peruvian EEZ	91...94	Max. 1000 mm	468 in 1 <sup>st</sup> 252 in 2 <sup>nd</sup> yr	MPA	Argüelles (1996)
-	-	-	paralarvae: exp. growth	Statolith	Yatsu (2000)
Peruvian EEZ	92	220/354d, 474/965 mm	786...995	Statolith	Argüelles et al. (2001)
GoC	95...97	386d, 875 mm	827	Statolith	Markaida et al. (2004)
GoC	95...02	<sup>2)</sup> 2.3...2.8 yrs 76...960 mm	<sup>3)</sup> 266...399	MPA	Nevárez-Martín et al. (2006)
Pacific off Pen. Baja California	04	♀ 433 d, 830 mm ♂ 391 d, 690 mm	♀ 762 <sup>4)</sup> ♂ 765 <sup>4)</sup>	Statolith	Mejía-Rebollo et al. 2008

<sup>1)</sup> in Argüelles et al. (2001); <sup>2)</sup> calculated from K; <sup>3)</sup> mean growth rate; <sup>4)</sup> calculated from max. daily growth rate of 20 day intervals

The most extreme values for longevity found in past studies are a maximum of four years and more assumed by Nesis (1970) for specimens above 500 mm ML and a life time of several months found by Argüelles et al. (2001) for specimens maturing at small ML. Minimal and maximal growth rates lie between 200 and 995 mm/year that again were found by Nesis (1970) and Arguelles et al. (2001). Although examples exist where the

results of modal progression analysis and otolith/statolith analysis are consistent (e.g. *Ty-santoteuhtis rhombus*, see: Nigmatullin et al. 1995, Miyahara et al. 2006), often high discrepancy between the results of the two methods of age evaluation has been described (fish populations e.g. Morales-Nin 1989a, b, Hammers & Miranda 1991; cephalopod populations e.g. Arkhipkin et al. 2000, citations in Jackson et al. 2000, Markaida et al. 2004). The results of studies on the growth parameters of *D. gigas* of the Peruvian HCS are no exception: compared to the statolith-analysis of Argüelles et al. (2001), longevity found by a MPA-approach in an earlier study (Argüelles 1996) is around two times higher.



*Figure IV-18 Study area with sketch of Humboldt Current and Equatorial Under Current (EUC) as well as the schematic mean location of relevant water masses and the Niño 1+2 monitoring area; TSW: Tropical Surface Waters; ESW: Equatorial Surface Waters; SSW: Subtropical Surface Waters, MW: Mixing waters*

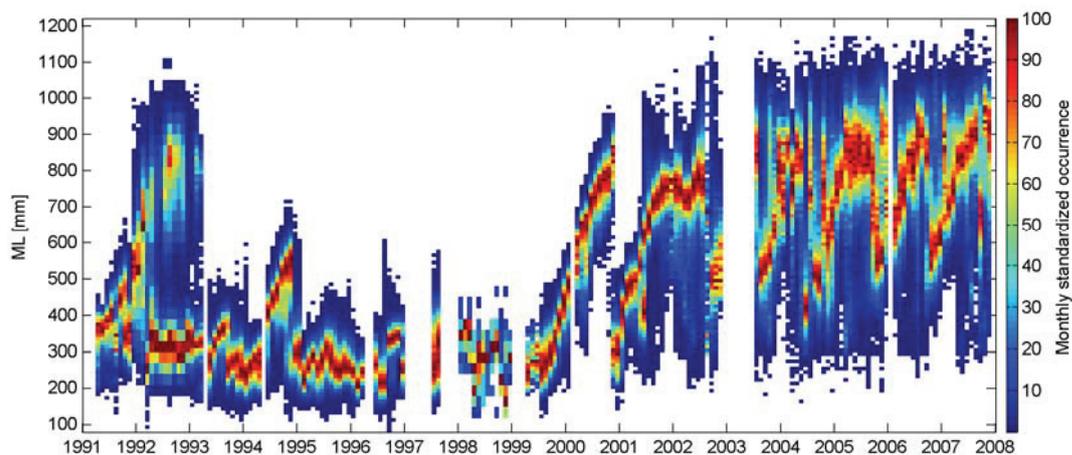
As was proposed for another squid, *Loligo forbesi* in Scottish waters (Pierce et al. 1994) it is assumed here that variable growth rates could be a possible source of differing growth rates in previous studies (Table IV-2). In case of *D. gigas* such variability has not been taken into account until now; the main reason certainly being the fact that the data available in studies cover only short periods. Main objective of this work therefore is to identify the individual cohorts of the Peruvian population of *D. gigas* between 1991 and 2007 and determine their growth rates and longevities. Variability of growth parameters is ex-

pected and analysed to relate it to prevailing environmental conditions and the results of previous work. Additionally, possible sources of the bias for the often described discrepancies between length-frequency analysis and statolith analysis used for the evaluation of age and growth are discussed.

### 3.3 - Data and Methods

Length-frequency data were taken by onboard technicians of the IMARPE monitoring program of the industrial *D. gigas* fishery realized by international fleets in the Peruvian EEZ (Figure IV-18) from 1991 to 2007 and contain over 4.3 Mio cases. Individual dorsal mantle lengths (ML), commonly used as an indicator for total length of squids, were measured to the closest millimeter. All data points collected throughout each calendar month in the entire study period were integrated to obtain a series of 175 month of length-frequency data grouped in 10 mm size classes.

For the length-frequency analysis (LFA) the original data of each month was standardized (maximal value of each month = 100) and plotted in histograms. For an overview, all months were plotted in a Hovmöller diagram where the standardized occurrences of the monthly length-frequencies are translated to colours and each column represents one month (Figure IV-19).



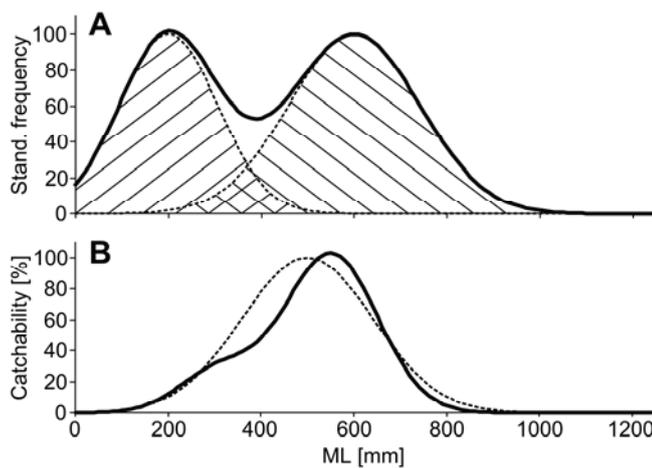
**Figure IV-19: Hovmoeller plot of standardized monthly occurrence of 10 mm ML-classes (max. value of each month = 100)**

In the modal progression analysis (MPA) the centres of the modes (i.e. the maximum value of each mode) representing the cohorts in each month obtained by the LFA were overlaid to a Hovmoeller plot that was recalculated from the modes obtained by LFA for each month and then linked visually to obtain all modes of a specific cohort.

For the decomposition of the monthly length-frequency distributions the model

$$Occurrence_{ML} = \exp\left(-\left(\frac{ML-a}{b}\right)^2\right) \cdot \sum_{i=1}^n c_i \cdot \exp\left(-\left(\frac{ML-d_i}{e_i}\right)^2\right)$$

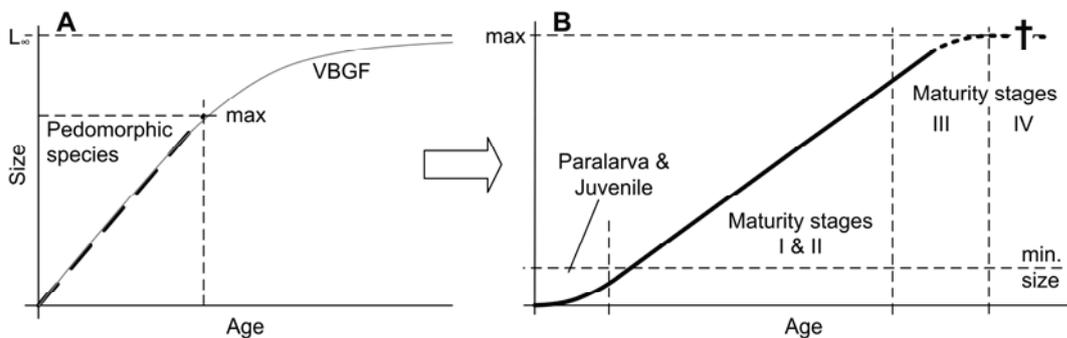
was used, where *a* through *e* are the parameters describing a number of Gaussian functions to calculate the occurrence for each *ML*. The first part of the formula, the Gaussian observation function, is employed in case that an observation bias is identified (hypothetical example shown in Figure IV-20) that is the result of size-dependent catchability of the deployed fishing gear. The Gaussian observation function corrects the introduced observation bias by altering the result of the observed length-frequencies to the underlying real modes. If an observation bias was not identified this part of the model was simply set to one. Start points for the Gaussian models of each cohort were selected graphically and then were fitted to the overall monthly LF-occurrence using a Matlab routine. Different numbers of modes (i.e. cohorts present) with and without jig bias were fitted to the data of each month and the resulting models were carefully compared using correlation coefficient and error distribution plots to identify the best model.



*Figure IV-20: Example of differences between real and observed length-frequency distribution; A) cohorts (broken line enclosing shaded areas) and resulting real length distribution (black line); B) observed length frequency distribution (black line) due to size-selectivity of employed jig (broken line).*

The form of the progressing modes of jumbo squid do not show the asymptotic form of the von Bertalanffy growth function (VBGF) but indicate a more linear growth (Figure

IV-19). Existing studies on the growth function of cephalopods are not consistent and range from exponential to linear and asymptotic functions with and without the incorporation of seasonal oscillation (e.g. Jarre et al. 1991, Pauly 1998, Masuda et al. 1998, review of Semmens et al. 2004, Miyahara et al 2006). Often, for adults non-asymptotical (see Jackson et al. 2000) or pseudo-linear growth has been postulated or can be identified in published work (e.g. Arkhipkin & Murzov 1987 in Nigmatullin et al 2001, Masuda et al 1998, Yatsu 2000). This has been attributed to the pedomorphic life history of cephalopods (Rodhouse 1998, Hatfield 2000), i.e. sub-adult maturation (Figure IV-21 A). Together with the exponential growth proposed for ommastrephid paralarvae (Yatsu 2000) and cephalopod senescence (Anderson et al. 2002), i.e. death shortly after the completion of the first spawning cycle before reaching the asymptotic part of the VBGF (Pauly 1998), a pseudo-linear growth function results for coleoid cephalopods (Figure IV-21 B). This composite growth function is very similar to the basic general growth model (BGM) proposed by Lipinski (2002). The fundamental critique of Day and Taylor (1997) on the use of an overall VBGF without considering reproduction processes (but also other processes) supports the here used combined function.



**Figure IV-21:** A) relation between von Bertalanffy growth function (VBGF) and assumed quasi-linear growth function of pedomorphic species; B) resulting growth function for three main life stages of *D. gigas* with exponential growth for paralarvae/juveniles and reduction of growth rate due to formation of reproductive tissue before death; min. size is size-at-first-capture of the Peruvian jumbo squid fishery.

Data used in the present work due to mean size of first capture does comprise very little information on specimens below a ML of around 150 mm (see Figure IV-19). Therefore, to analyze the modal progression a simple linear regression was applied to the identified means of modes of each cohort corresponding to the second growth phase of Lipinski's BGM which has been considered the longest and most important in cephalopod life (Lip-

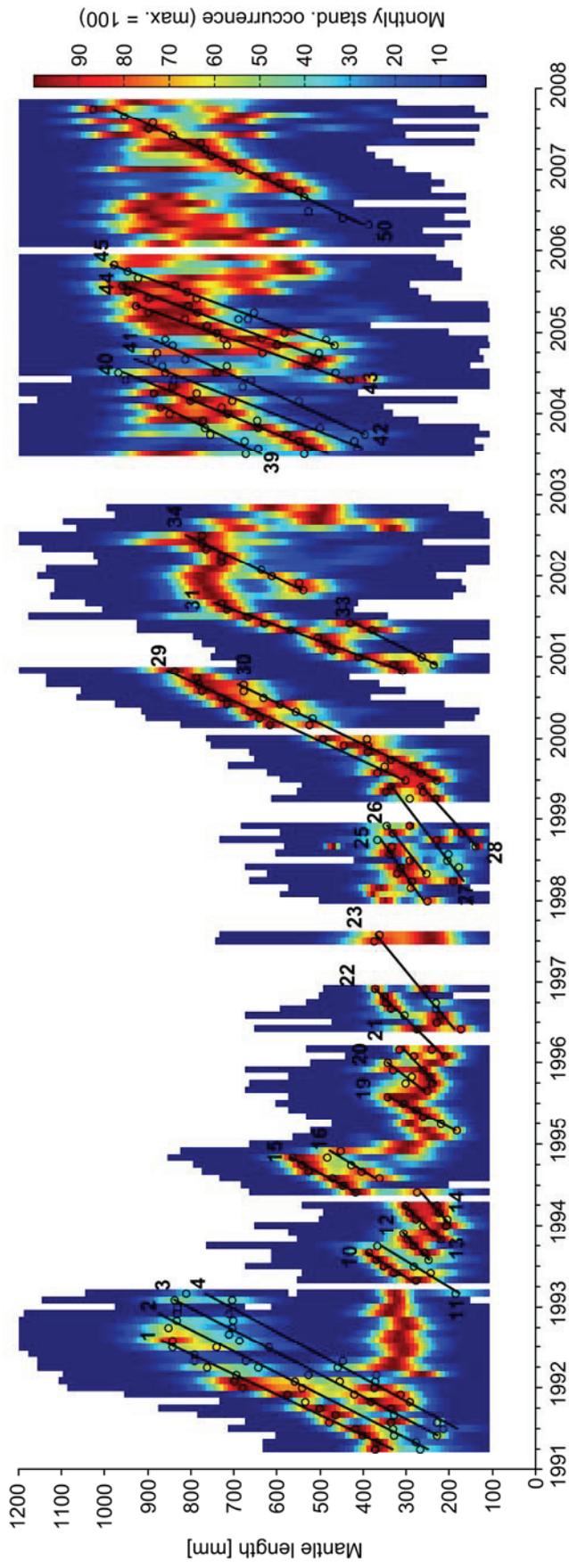
inski 2002). The cohorts' mean growth rate is then equal to the slope of the regression line resulting from the centres of all modes belonging to a cohort. Ignoring exponential growth of paralarvae (Yatsu 2000) the interpolation of the regression to ML zero results in the latest possible hatching date of each cohort. Maximal age of a cohort was calculated by subtracting the calculated hatching date from the month of the largest mode of the cohort. Seasonal oscillation has not been included in the growth function.

For each month the number of cohorts entering the system in the next 12 month was determined. Overall number of cohorts as well as mean growth rate, maximal mean size (i.e. the mean of the largest mode) and mean longevity for each season were calculated.

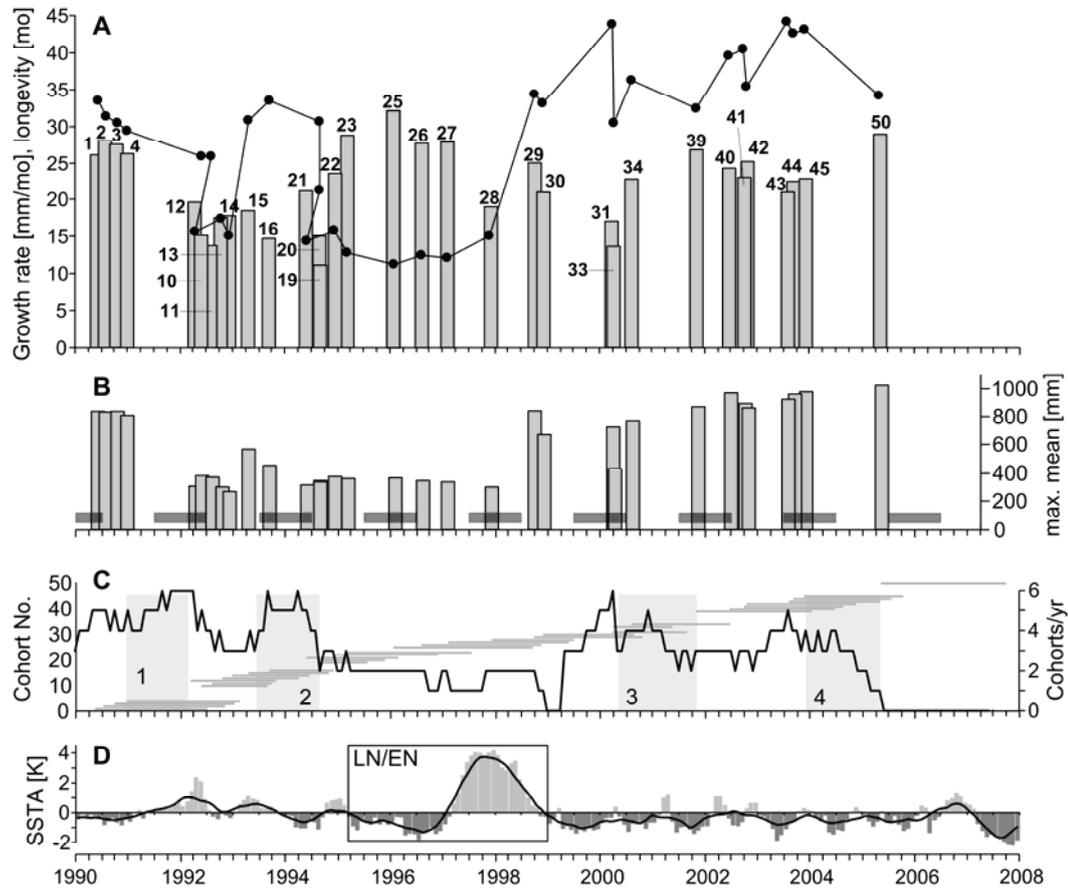
### **3.4 - Results**

In 60% of the 175 month the amplified model to correct observation bias was used in the length-frequency-analysis. All in all 33 cohorts have been identified in the period from April 1991 to December 2007 and the cohorts do not show a uniform picture with respect to its succession, terminal size and growth rates (Figure IV-22, Figure IV-23 and Table IV-2). Three main periods can be identified: the first until around 1994, the second from 1995 to 1998 and a third that covers the 2000s. The growth rates of the cohorts illustrated in upper panel of Figure IV-23A show these periods clearest but they can also identified in terminal size (Figure IV-23B) and number of cohorts per 12 months (Figure IV-23C). The first period shows a discontinuity in early 1992 when growth rate suddenly drops to values similar to those of the second period. Longevity is more stable and at first appears relatively independent of terminal size with most cohorts showing a life time of nearly two years. The shortest life time of just above 11 months found for cohort 17 occurs at the end of the first period just before the drop in growth rates and prolonged life time. It is remarkable that the following cohorts of the second period that all live two to three times longer, are not growing larger than this cohort. The longest lifetime of over 32 month was calculated for cohort 23 that is one the smallest of all identified cohorts.

The maximal size (i.e. the centre of the largest mode belonging to a cohort) of the different cohorts is similarly variable (Figure IV-23 B and Table IV-2). Cohorts with maximal sizes from 274 to 1024 mm were identified and especially during the 2000s a gradual in-



*Figure IV-22: Cohorts identified by LFA and mean linkage with underlying monthly length-frequencies recalculated from identified Gaussian modes; discontinuous numbering of cohorts indicates supposed missing cohorts not clearly identified; open circles are the means of the identified modes.*



**Figure IV-23: Growth parameters of the identified cohorts shown in Figure IV-22; A) Growth rates (line and points) and longevity (bars); back calculated time of hatching of each cohort is given by location of points and bars in time axis; B) centres of largest modes belonging to one cohort, i.e. the maximal. mean size of identified cohorts; horizontal bars represent austral spring/summer months (October to March of the following year); C) plot of temporal sequence of identified cohorts in the study area (bars) and number of cohorts entering the system in the following 12 month (line); grey shaded boxes indicate periods with presumably missing cohorts due to low number of identified modes (periods 1 and 2), missing data (period 3) and too many modes that prevent a clear identification and assignment to specific cohorts (period 4); D) sea-surface temperature anomalies (SSTA) of the monitoring area Niño 1+2 (see Figure IV-18)**

crease of maximum cohort size can be noticed. Cohorts that reach large sizes (675 mm and more) occurred during 1991 and in the 2000s while cohorts that stay small (386 mm and less) were found from 1992 to 1998. The exception in this period are two cohorts in 1993 that reach 562 and 450 mm and one cohort (33) that reached only 425 mm during the 2000s where other cohorts reached sizes well above 600 mm.

**Table IV-3: Growth parameters and back-calculated hatching date of the identified cohorts; discontinuous numbering of cohorts indicates supposed missing cohorts that were not clearly identified; please notice that hatching seasons are austral seasons.**

Cohort	Max.size [mm]	GR [mm/mo]	Age [mo]	Hatching date	Hatching season
1	841	33	25.9	1990.42	autumn
2	832	31	28.0	1990.58	winter
3	836	31	27.5	1990.79	spring
4	809	29	26.2	1990.99	spring
10	386	26	15.2	1992.40	autumn
11	365	26	13.8	1992.60	winter
12	304	16	19.6	1992.28	autumn
13	299	17	17.6	1992.79	spring
14	273	15	17.8	1992.93	spring
15	562	31	18.5	1993.29	autumn
16	450	33	14.7	1993.69	winter
19	341	31	11.1	1994.66	winter
20	342	21	15.1	1994.66	winter
21	314	14	21.1	1994.41	autumn
22	372	16	23.6	1994.95	spring
23	361	13	28.6	1995.20	summer
25	366	11	32.1	1996.08	summer
26	345	12	27.6	1996.61	winter
27	335	12	27.8	1997.10	summer
28	300	15	19.0	1997.92	spring
29	836	34	24.9	1998.76	spring
30	675	33	20.9	1998.92	spring
31	728	44	17.1	2000.24	summer
33	425	31	13.7	2000.28	autumn
34	773	36	22.7	2000.61	winter
39	870	32	26.7	2001.86	spring
40	967	40	24.2	2002.48	autumn
41	889	41	22.9	2002.76	spring
42	858	35	25.2	2002.82	spring
43	925	44	21.0	2003.59	winter
44	957	43	22.5	2003.71	winter
45	976	43	22.8	2003.93	spring
50	1024	34	28.8	2005.35	autumn

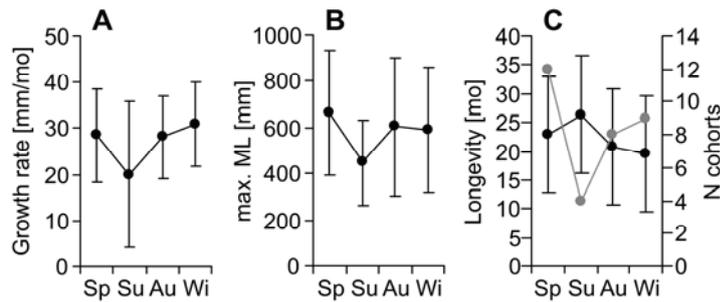
In four periods (represented by the grey boxes in panel C of Figure IV-23) for different reasons no cohorts could be identified. During periods one and two the terminal ML of the cohorts were just above the minimum size vulnerable to fisheries. Of these cohorts only the last modes were available for the MPA and no reliable regression could be found due to the low number of modes (Figure IV-22). Nevertheless, in both periods the stable ML of the available modes indicate a very continuous reproduction and succession of new cohorts. During period four in the years 2004/05 the problem why cohorts could not

be identified was the contrary: too many modes identified made particulate cohorts indistinguishable. For period three (2002/03) no data was available and although several cohorts seem to progress through that time, these were not to be determined definitely. The discontinuous numbering of the identified cohorts indicates the supposed number of not identified cohorts.

The number of cohorts entering the system in one year is not constant (Figure IV-23, black line in panel C). Number of new cohorts was found to be between 0 and 6; the overall mean of new cohorts per year is 3.18 ( $\pm 1.41$ ). Again three periods can be identified: during the early 1990s four to five cohorts entered in the following 12 month, in the second period from 1995 to 1998 this number dropped to two and rose again to three in the third period in the 2000s. During the first period in 1992 a short reduction to 3 cohorts can be observed. For this analysis the unclear cohorts that have not have been used for the MPA and are not represented in Figure IV-23 A were added.

The second period and the short break during the first period can be related temporally to the period of the LN/EN-event of 1996 to 1998 and EN 1992/93 respectively that introduced high physical variability in the Peruvian HCS as indicate the SST-anomalies of the Niño 1+2-area shown in Figure IV-23D. The lag between biological response and physical environment that seems to exist results from the fact that cohorts in panel A are drawn in the x-axis at their respective hatching dates, i.e. the impact of EV during their lives is lying ahead. This can be observed in Figure IV-23C where the vertical bars representing the cohorts with the lowest growth rates (cohorts 12 to 14 and 21 to 28) are located exactly in the LN/EN-period.

Cohorts 29 and 30 and even more cohort 31 are the cohorts that are progressing through time clearly separated from others (Figure IV-22). Especially in the latter cohort the linear growth and a final reduction of growth rate during or after maturing as proposed (Figure IV-21) is apparent. At two points, in the beginning of 1994 and in mid 1999, during a period of cohorts belonging to the group of small-size-maturity one or two following cohorts grow much larger than their predecessors and especially in the case of the 1999 cohort an interruption of reproduction succession can be observed.



**Figure IV-24:** Seasonal means of growth rates (A), largest mode (B) and longevity (C) of the identified cohorts; grey line in C is number of cohorts considered in each season to calculate means of all parameters.

The linearly back-calculated hatching dates of the cohorts reveal that reproduction is not restricted to austral spring/summer but occurs throughout the year (Figure IV-24C and Table IV-2). Although the season with the highest number of cohort is spring, autumn and winter show only slightly less reproductive activity. Summer is the only season with a strongly reduced number of cohorts. The seasonal means of growth rates, maximum size reached and longevity of cohorts born in different seasons are not significantly different although mean growth rate and mean maximum size of summer born cohorts are lower than those of the other seasons. A tendency of shorter life time for cohorts born during the other, cooler months can be noticed. The characteristics of summer hatched cohorts with low growth rates, small terminal size and following elevated longevity are similar to those of cohorts hatched during warm periods, i.e. EN.

### 3.5 - Discussion

A number of studies have been published on the variability of growth rates and size-at-age in general (e.g. Atkinson & Sibly 1997). Intra-annual and intra-cohort variability of growth rates of coleoid cephalopods with respect to seasonal temperature changes is well known (Pauly 1985, Forsythe & Van Heukelem 1987, Bettencourt et al. 1996, Dunn 1999, Hatfield 2000, Wood & O'Dor 2000, Villanueva 2000, review of Semmens et al. 2004) but inter-annual variability of growth rates has been reported only for *Loligo forbesi* in Scottish waters (Pierce et al. 1994). Other studies on inter-annual variability of growth parameters and longevity are rare and in these inter-annual variability has been considered rather unimportant (Arkhipkin & Laptikhovskiy 1994, Pecl et al. 2004). The results of the present work show that at least for *D. gigas* inter-annual variation of growth

rates is very marked and is assumed to respond to changes of the environmental conditions of the northern HCS. Intra-annual variations – although noticeable – are not significant. Inter-annual variability of growth parameters that was supposed to be related to changing biotic and abiotic factors was also found for jumbo squid of the Gulf of California (Nevárez-Martínez et al. 2006) but less marked as here.

The mentioned work of Nevárez-Martínez et al. (2006) and one on *L. forbesi* (Pierce et al. 1994) variable growth rates to our knowledge have not been incorporated in evaluations of growth parameters. Exceptions are the examples of sinusoidal oscillating VBGF to reproduce regular seasonal growth variability but these do not reproduce inter-annual variability. One reason could be that the period covered by the data used in such studies usually is too short to discover such variability. However, the present results suggest that inter-annual (i.e. inter-cohort) variability of growth rates must be considered as it is an essential effect of population dynamics that is related to changing environmental conditions. This is especially important when analyzing growth parameters of cephalopods or other species that show high phenotypic plasticity in response to EV (Boyle & Boletzky 1996) and when using multi-annual timeseries that cover periods of marked EV. Shortfall in this sense in earlier investigations on cephalopod growth using MPA may have contributed to the hypothesis that LFA and MPA are not suitable to study growth of cephalopod populations (e.g. review of Semmens et al. 2004).

The very low growth rates found here associated to the very cool (LN) and the very warm (EN) environmental conditions suggest a mixed origin of the variability of growth parameters. It is assumed that low growth rates during LN are the consequence of lower environmental temperatures due to physiological reasons as has been described for other species (e.g. Atkinson & Sibby 1997, Hatfield et al. 2001). Especially during the paralarval phase the individual development of cephalopods is affected by environmental temperature (Lipinski 2002).

The low growth rates during EN (the warming events of the southern oscillation) however, can not be explained on a physiological basis, as growth during warmer times should be higher. As growth processes in cephalopods are not only influenced by temperature but also by the availability of food (e.g. Mangold 1987, Lipinski 2002, Forsythe 2004, Miyahara et al. 2006), it is assumed that the low growth rates of the cohorts during

EN have an indirect ecological cause that is related to the energy content of the ecosystem, i.e. the food availability and the general lower performance of the pelagic trophic system in the HCS (Ayón et al. 2008a,b, Tam et al. 2008, Taylor et al. 2008). In case of monocyclic organisms like *D. gigas* and other cephalopods (Rocha et al. 2001) the onset of maturation again governs the maximum size and longevity of an individual. Here we found that large terminal sizes were reached only by those cohorts that also show high or very high growth rates supporting Mangold (1987) who proposed the dependency of the onset of maturity from food availability.

Cohorts that fulfil their life cycle during the LN/EN-period are clearly different from the other cohorts. Due to the very low growth rates their longevity is as high or even higher as that of the largest cohorts but their maximal size is among the smallest. This must necessarily lead to different size-at-age during such extreme conditions and to major implications for assessment and management of *D. gigas* during such periods.

The occurrence of cohorts with gradually changing maximum sizes in the range from 274 to 1024 mm (Figure IV-23B and Table IV-2) make the existence of three separated groups of size-at-maturity as proposed before (Nesis 1983; Nigmatullin et al. 2001) doubtful at best. Apparently *D. gigas* is able to respond to unfavourable environmental conditions by reducing size and growth rate to reduce its quantitative nutritional requirements. A very similar gradual transition between size extremes was also found calculating seasonal size-at-maturity and an individual maturity index for jumbo squid in the Peruvian EEZ (Tafur et al. *subm.*).

The subsequently hatched cohorts 19 and 20 and 21 have nearly the same maximum size but differ in growth rate and longevity. The differences of the otherwise comparable cohorts suggest the influence of another important driver that has not been covered by the analysis in this study. Cohort 21 was growing slower than the others and was becoming much older than the latter cohorts (21.1 month compared to 15.1 and 11.1 month, see Table 2). However, the back-calculated dates of eclosion reveal that all three cohorts hatched within a period of less than two month. Cohort 21 that according to its growth parameters belongs to the LN/EN-groups of cohorts even hatched before the cohorts 19 and 20 that are thought to belong to the pre-LN/EN-period (Figure IV-23). We assume that this is the result of a limited spatial distribution of at least some cohorts in the Peru-

vian EEZ that made it possible that cohorts 19 and 20 still dwelled in pre-LN/EN-conditions while cohort 21 already experienced the conditions which all cohorts afterwards experienced for the following two years. Similar changes of growth parameters of successive cohorts can be observed for the long-lived cohort 12 and the short-lived cohorts 10 and 11.

These findings support the hypothesis of Keyl et al. (2008) who assumed that life history traits of different *D. gigas* groups are dependent of the differently productive watermasses and their distribution. There, cool and warm waters inside and outside the Peruvian EEZ respectively were thought to be the origin of different size-at-maturity. Here, we assume that the waters inside the EEZ are also inhomogeneous. The development of an EN and the resulting spatial expansion of warmer water masses in the northern Humboldt Current System is not instantaneous. It propagates along the coast from north to south during several month and according to the strength of the event (Bertrand et al. 2008, DeWitte et al. 2008), i.e. the northern part of the HCS and its biota may experience already EN conditions while the central and southern part remain mainly unchanged still. To clarify the origin of differences in growth-related parameters of coexisting cohorts a spatial explicit analysis is necessary in future studies.

In the past annual cohort number of *D. gigas* was reported to lie between one (Morales-Bojorquez et al. 2002) and 5 cohorts (Ehrhardt et al. 1983) in the GoC. Here, the period with the lowest value of entering cohorts was found to be the period from 1995 to 1998 corresponding to the LN/EN-event (Figure IV-23) proposing also a dependency of the reproductive frequency from environmental conditions.

Often discrepancies have been found between the results obtained by statolith analysis and modal progression analysis (MPA) based on the modal decomposition of length frequency data. This was also found to be the case for *D. gigas*. The present study identified four cohorts in the period from 1991 to 1994 and found longevities of one to two years, supporting a previous study of Argüelles (1996) that used MPA. It contradicts the statolith analysis of Argüelles et al. (2001) that found a longevity of roughly half a year to one year. Similar dichotomy was found for cohorts of 2002 that here were found to live roughly 2 years compared to the results of a statolith analysis of individuals of this year that had a longevity of 1 year (unpublished data, C. Goicochea, IMARPE). Stronger dis-

crepancies still were observed for cohorts of 1997 and 1998. Results of the present study found a longevity of between 19 and 32 month that is opposed to preliminary results of a statolith analysis that found less than 200 rings for mature individuals ( $n = 20$ ) of the same period and the same size (unpublished data, J. Argüelles, IMARPE). In general, all results obtained by statolith analysis conclude with results of other studies on *D. gigas* in the EPO of both hemispheres using this method as do those using MPA when compared to other MPA of length-frequency-data (see Table 1).

Two groups with opposite opinions on growth and longevity of cephalopods have been mentioned by Jackson et al. (2000). One group that uses the MPA-method “ELEFAN” and that considers cephalopods to be relatively long-lived and to grow according to the VBGF sees cephalopods as fish. Other researchers, belonging to the “statolith”-group, see cephalopods fundamentally different from teleosts and found this taxon to be shorter-lived and exhibiting linear or exponential growth. However, similar discrepancy between the two methods, although less pronounced, has also been found in analysis of fish growth (e.g. Ralston & Williams 1988, Morales-Nin 1989a, b, Hammers & Miranda 1991). The often applied ELEFAN I (included in the program FiSAT II, obtainable from FAO) was not used, as this software is not able to deal with the linear growth function proposed here nor with a changing number of cohorts per year or the observation bias (see below).

Reasons for biased results have been put forward for both methods. A relatively vague argument for the underestimation of real age by statolith analysis has been the elevated growth rates itself that were assumed to be impossibly high (Jarre et al. 1991). A more severe doubt in case of the statolith analysis is that for many cephalopods, among these *D. gigas*, a confirmation of the assumed daily formation of statolith rings is missing. Various factors have been reported to affect the accretion of otoliths and statoliths and their legibility. The accretion of “blurred” areas without rings found in the areas towards the margins of statoliths of older specimens has been assumed to be a reason of underestimating real age in case of the otolith/statolith analysis (Pauly 1998, Balgos & Pauly 1998) and later been confirmed in experiments (Bettencourt & Guerra 2001). One of the outstanding features of jumbo squid is its remarkable tolerance of hypoxia that not only allows it to use the oxygen-minimum layer (OML) in the oceans as shelter from predators as e.g. small pelagic fish do but also to move and hunt actively for hours under hypoxic

conditions (Gilly et al. 2006, Zeidberg & Robison 2007, Rosa & Seibel 2008). Considering that oxygen-availability not only affects otolith formation (Sepúlveda 1994) but also that of statoliths (Lipinski 1993, Pauly 1998) we assume that the daily or nearly daily visits to the OML of jumbo squids cannot be without effect on their statolith formation and is causing “bleached” areas and missing statolith rings. Other factors like temperature (Bettencourt & Guerra 2001), body-size (Hüsey 2008a) and feeding level (Spratt 1979, Kristensen 1981 in: Zumholz 2005, Hüsey 2008b) affect the formation of otoliths and possibly also that of statoliths. More bias is introduced during the initial paralarvae life stage where paralarval statoliths do show “indistinct” increments as has been shown in a growth experiment (Yatsu 1999).

On the other side for MPA it has been proposed that migration (Hatfield & Rodhouse 1994) and the existence of micro cohorts that may not be distinguished (Caddy 1991) provoke that length-frequency data are interpreted in a way that leads to underestimation of growth rate and thus longevity. Wrong growth functions as well as errors in identifying the modal progress due to inappropriate temporal resolution or pooling of length-frequency data, too, have been assumed to result in similarly skewed growth rates and longevity (Pierce & Guerra 1994, Jackson et al. 2000). In case of the present work it is assumed that the pooling of available data of the entire Peruvian EEZ into monthly time increments minimizes both problems. The study area possibly enfolds great parts if not all migration and the monthly time increment compared to longevity from roughly one year to nearly three years is well chosen.

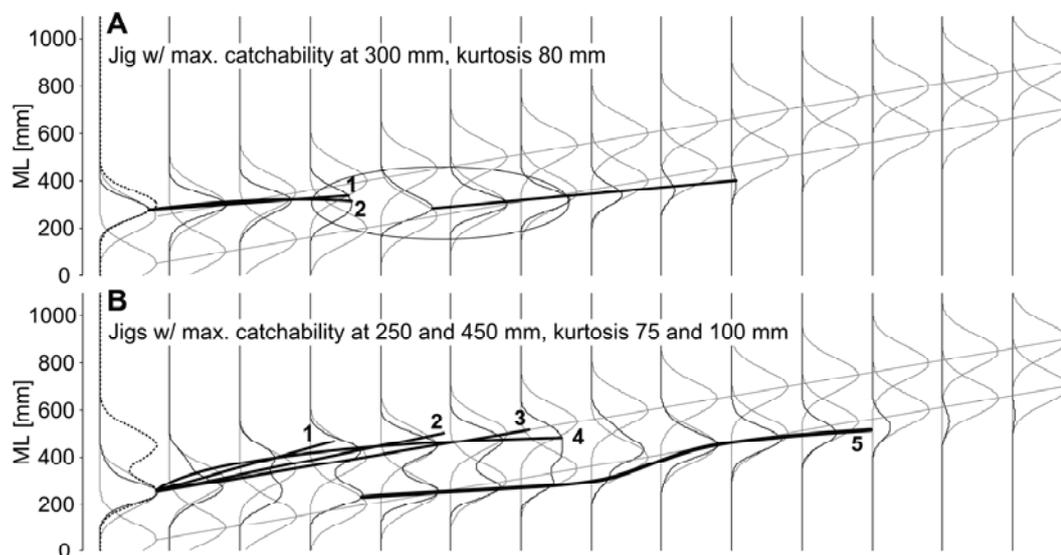
The jigs used in many squid fisheries and other squids are highly size specific. Preliminary results of a study with four jig sizes (small, medium, large and extra large) show an exact Gaussian function for the selectivity with maximum catchability at 300, 310, 540 and 830 mm respectively (J. Argüelles, IMARPE, unpublished data). The fact that the length-frequency dataset of each month is pooled from a great number of fishing operations of different ships using a number of jig sizes throughout one month should mitigate the problem of observation bias introduced by the size specific catchability of the jigs. The high number of cohorts per year found for *D. gigas* results in a continuous entry of new cohorts that in parts must be underestimated when observed (i.e. fished) with one size of jig that covers only parts of the whole size range. This is shown in Figure IV-20 and explains why in the analysis of the monthly length frequency in 60% of the 175

months the amplified LF-model was needed to correct the observed modes to the supposedly real values. A visual comparison of the Hovemoeller plots of the standardized original dataset (Figure IV-19) and the one corrected by the observation bias (Figure IV-22) demonstrates the high overall similarity of the two plots but a higher coherence of the modes of subsequent months is observed in the latter case.

Parameters of the observation bias part of the model are variable reproducing the great number of jig sizes employed in the fishery and the fact that the jigs are changed without much delay according to the size of specimens primarily available at every fishing operation (anecdotal reports of on-board technicians). Such a variable use of jig sizes seems logical as economic requirements prevent to fish an extended time on a sub-optimal level which would occur when using sizes of jigs not adequate for the actual size of the specimens found during a fishery operation. However, this also implies that if several cohorts with different sizes are present those cohorts that are less abundant must be underrepresented in the catch if: (1) only one jig size is used at a time or (2) the relative numbers of different jig sizes employed are not conform with the relative number of occurring size classes.

A simple graphical comparison of two subsequent hypothetical cohorts with linear growth was conducted to better understand if and to what extend erroneous growth rates or growth functions can result from biased observation. Observations with one and two jig sizes were applied. When using one jig only the resulting growth rate is clearly lowered, the form of the growth function may be misinterpreted and the cohorts at least in parts of the size range are difficult to distinguish (Figure IV-25A). When using two jig sizes the bias is reduced but the resulting growth rate in this case can be both lower and higher than the real one. The obtained growth rates appear to be different when considering size classes below the size range covered by the jigs, in this range and above this range. This could not only lead to wrong growth rates but again also to a misinterpretation of the form of the growth function and even to the wrong conclusion of seasonally oscillating growth that does not exist (apparent growth function 5 in Figure IV-25B). To prevent wrong results when using MPA it must be secure that either the gear used covers the largest part of the size range of the species of interest or, as in the present case, if this is not given a correction of the observation bias must be conducted. If this is not respected results of a MPA in all likelihood will be wrong and we assume that this in the past has of-

ten been the case. This effect must be especially valid when using data obtained from jig fisheries that have a two-sided size-selectivity, i.e. towards too small and too large specimens in a population. Nets on the contrary usually exclude only small individuals which could explain that discrepancies between statolith analysis and MPA are less pronounced or non-existent in case of fish. The above mentioned consistence of the two methods in case of the diamond squid *Thysanoteuthis rhombus* is interesting in this context: one study describes the use of trawl nets and jigs of “various kinds” (Nigmatullin et al. 1995) and the other angling and nets (Miyahara et al. 2006). In both cases the employed fishing gear reduces or abolishes the size-specific catchability and consequently observation bias.



**Figure IV-25:** Two hypothetical cohorts with linear growth through 14 time increments (grey lines); bias in growth by observation through fishery gear (here jigs) with different size-dependent catchability (broken black lines in first time increment) and resulting growth functions (real: grey lines; observed: black lines); x-axis of each time increment is frequency of occurrence per size-class; numbers of observed growth functions indicate different types of growth functions; A) observation with one jig-size; ellipse indicates unclear area; B) observation with two jig-sizes.

The present study of LF-data of the Peruvian *D. gigas* in its methodology is using a novel form of the modal progression analysis (MPA) as the monthly length-frequency data (Figure IV-19 and Figure IV-22) obviously indicated linear growth of the cohorts. This led to the rejection of the VBGF and the use of a linear growth function. Nevertheless, the present results that are similar to those of the MPA of Argüelles (1996) for the cohorts in 1991 are not consistent with that of the statolith analysis of the same cohorts carried out

by Argüelles et al. (2001). Due to the employed correction of the observation bias in the MPA it is assumed that in case of *D. gigas* of the Peruvian HCS varying accretion processes in dependency of oxygen-level and food availability may be one source of the observed discrepancy between the methods.

Further work will have to be done to finally clarify the reasons of the dichotomy produced by the two growth determination methods. The verification of the widely accepted hypothesis that statolith rings in squids are formed on a daily basis that is based on a relative small number of well-studied species is most important. However, due to the difficult and until now impossible long-time cultivation of jumbo squid any rapid solution at least for this species is difficult to achieve. Until now it was not possible to keep *D. gigas* in captivity for more than 12 days (W. Gilly, Hopkins Marine Station, personal communication) and the possibility to conduct controlled experiments to investigate statolith formation is therefore highly limited or even impossible. We assume that the joint application of electronic tags on a high temporal resolution (e.g. pop-up satellite tags, see Gilly et al. 2006) and micro- or nano-scale chemical analysis using mass spectrometry (e.g. NanoSIMS, see Zumholz et al. 2007) may overcome this limitation and advance our understanding in the formation of the microincrements of statoliths. Future research in this direction is recommended.

The analysis of regular growth structures of the gladii or the mark-recapture methods were proposed as alternatives to help clarify the discrepancy found between results of MPA and statolith analysis. However, the first method has similar limitations than the use of statoliths. Until now it has rarely been employed, temporal frequency of the formation of the growth marks is not verified and the formation of these is considered to be strongly temperature affected (Bettencourt & Guerra 2001) The latter method in case of the abundant oceanic squid *D. gigas* also seems difficult to be implemented due to the special geographic and fishery situation at least in the northern HCS.

### **3.6 - Conclusions**

Growth parameters were found to be highly variable and showed a strong dependency of environmental conditions. It is assumed that a mixed impact of the factors temperature and food availability control growth rates and the onset of maturation that together define longevity and maximal size. The possibility to alter growth rate and maximal size that is

related to size-at-maturity allows *D. gigas* to react to productivity and temperature changes of its ecosystem. Under favourable environmental conditions it not only more than triples its maximal size and growth rates but also increases its reproduction frequency to optimally use available energy. The biomass increase found earlier (Keyl et al. 2008) is then the consequence of bigger and faster growing specimens that additionally more repeatedly reproduce.

The maximal size of Peruvian jumbo squid during the study period gradually varied between a lower and an upper extreme which makes the existence of distinct groups of size-at-maturity that have been proposed before (Nesis 1983, Nigmatullin et al. 2001) rather unlikely.

The present work on growth parameters using MPA as numerous studies before is not consistent with studies using statolith analysis. It has been proposed not to rely only on MPA but to use both methods instead (Caddy 1991) and this is especially true when using rather inflexible programs like e.g. ELEFAN for MPA. Nevertheless, when utilizing a tailored solution that allows (1) multiple cohorts per year, (2) the incorporation of inter-annual variability of growth parameters, (3) the selection of an adequate growth function and (4) the correction of observation bias introduced by restricted catchability in function of size, a MPA can be sufficient in case that statolith analysis is not possible. ELEFAN and any other method that insist on a specific growth function or constant growth parameters should not be used or at least revised extremely carefully with respect to its suitability in each specific assessment case. Statolith analysis on the other side relies on the formation of one ring in one day which often has not been directly verified. It hardly ever accounts for effects of environmental factors on the formation of the rings. Future research must be directed to clarify the exact reasons of the discrepancy of the two methods to obtain tenable results on age and growth parameters.

**Acknowledgements.** We thank all our colleagues at the IMARPE that kindly supported and advanced our work with their knowledge, experience and advice, especially those from the Marine Invertebrate Department and all on-board observers. We thank M. Wolff for his willingness to develop and tackle ideas with us during the elaboration of discussion. F. K. in parts was financed by CENSOR.



## 4 - Cannibalism in cephalopods

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**Manuscript accepted for publication in Reviews in Fish Biology and Fisheries**

## 4.1 - Abstract

Cannibalism refers to the action of consuming a member of the same species and is common in many taxa. This paper reviews the available literature on cannibalism in cephalopods. All species of the class Cephalopoda are predators and cannibalism is common in most species whose diet has been studied. Cannibalism in cephalopods is density-dependent due to their aggressive predatory and in case of the octopuses territorial nature. It also depends upon local and temporal food availability and of the reproductive stage. Cannibalistic behaviour is positively related to the size of both cannibal and victim. It can affect population dynamics of cephalopods in periods of low food availability and/or high population abundance. Cephalopods are generally restricted in their ability to store energy. It is thus assumed that cannibalism is part of a population energy storage strategy enabling cephalopod populations to react to favourable and adverse environmental conditions by increasing and reducing their number. Finally, we propose five orientation points for future research on cannibalism in cephalopods.

**Keywords:** Cannibalism, Cephalopods, Density-dependence, Food shortage, Population cycles

## 4.2 - Introduction

To kill and eat a member of the same species is common in animals of various taxa and occurs for different reasons. Cannibalism can provide a competitive advantage among juveniles and/or adults and may be beneficial for survival in periods of food scarcity (Fox 1975, Polis 1981, Caddy 1983, Calow 1998). Cannibalism induced mortality can reach up to 95% of a particular age class (Fox 1975) and is often dependent on the size of the predator (Polis 1981, Amaratunga 1983, Sauer & Lipinski 1991, Claessen et al. 2000, 2002). It constitutes an important link between processes from the individual to the population level (Claessen et al. 2002). The size range of prey that a predator can capture has been defined as the window of predation and in case of cannibalism as the window of cannibalism (Claessen et al. 2000, 2002). Although cannibalism is size-specific, exceptions are known. Generally, the relative size difference between victim and predator is more important than the absolute size. Species that pass through ecdysis (the moult of the exoskeleton) periods, have pupae stages or are able to attack in groups show size-

independent cannibalism that lead to the conclusion that cannibalism in general is the result of physical dominance (Polis 1981).

Cannibalism is thought to be an important mechanism of density-dependent regulation in aquatic animals as fish (Laevastu & Favorite 1988, Smith & Reay 1991, Fortier and Villeneuve 1996, Wespestad et al. 2000, Claessen et al. 2000, 2002, 2004), cephalopods (Caddy 1983, Aronson 1986, Dawe 1988) and crustaceans (Fernández 1999, Moksnes 2004). It produces feedback mechanisms that can lead a population towards a determined density and in that way can be an important component of natural mortality (Polis 1981, Caddy 1983, Smith & Reay 1991, Claessen et al. 2004, Jurado-Molina et al. 2006). Different effects on the dynamics of a population can result: it may (1) force a population into population cycles, (2) destabilize it and create deterministic chaos, (3) stabilize it, (4) result in bi-stability and/or (5) have effects on the size distribution resulting in bi-stability of size distribution (see Claessen et al. 2004). Studies in marine fish have shown that cannibalism can control recruitment and produce cycles of different population densities (Ricker 1954, Uzars & Plikshs 2000, Wespestad et al. 2000, Claessen et al. 2000, 2002, 2004). In general, the behaviour of the victim (as that of the aggressor) can be the reason for cannibalism and as behaviour often is density-related, the rates of cannibalism are often related to the number of encounters (Fox 1975).

Intra-cohort and inter-cohort cannibalism can be distinguished (Wootton 1990). Intra-cohort cannibalism occurs between conspecifics of approximately the same age, and is common in fish and cephalopods (Smith & Reay 1991, Wootton 1990, Hanlon & Messenger 1996). Mortality caused by this type of cannibalism reduces intra-cohort competition and increases growth rates (Crowley & Hopper 1994, Claessen et al. 2000). Together with inter-cohort cannibalism that is inflicted by large specimens on smaller ones of – usually – younger cohorts it gives an opportunity to decrease competition by reducing density (Claessen et al. 2000).

Both types of cannibalism are usually hetero-cannibalism (i.e. cannibalism on unrelated conspecifics) in contrast to filial cannibalism – a special form of inter-cohort cannibalism – that relates individuals to their own offspring. Filial cannibalism usually reduces the fitness of an individual and this type of cannibalism occurs only when the benefit of cannibalism for the cannibal is high (Thomas & Manica 2003). A special form of intra cohort

**Table IV-4: Intensity and categories of cannibalism of cephalopod species.**

Species	Inten.	Cat.	Source
<b>Order Nautiloidea</b>			
<b>Family Nautilidae</b>			
<i>Nautilus</i> sp.	incid.	inter	Arnold & Carlson 1986 <sup>1)</sup>
<b>Order Sepiida</b>			
<b>Family Sepiidae</b>			
<i>Sepia officinalis</i> Linnaeus 1758	comm.	intra	Castro & Guerra 1990 <sup>2)</sup> , Pinczon du Sel et al. 1997 <sup>3)</sup> , 2000 <sup>2)</sup>
<i>Sepia australis</i> Quoy & Gaimard 1832	high		Mqoqui et al. 2007 <sup>2)</sup>
<i>Sepia pharaonis</i> Ehrenberg 1831	comm.		Roper et al. 1984
<b>Order Teuthida</b>			
<b>Family Ommastrephidae</b>			
<i>Todarodes pacificus</i> Steenstrup 1880	comm.		Roper et al. 1984
<i>Todarodes sagittatus</i> Lamarck 1798	comm.		Quetglas et al. 1999
<i>Todaropsis eblanae</i> Ball 1841	comm.		Lordan et al. 1998 <sup>2)</sup>
<i>Ommastrephes bartrami</i> Lesueur 1821	high	inter	Roper et al. 1984, Lipinski & Linkowski 1988, Ivanovic & Brunetti 2004 <sup>4)</sup>
<i>Sthenoteuthis pteropus</i> Steenstrup 1855	comm.		Roper et al. 1984
<i>Nototodarus gouldi</i> McCoy 1888	high		Roper et al. 1984
<i>Dosidicus gigas</i> d'Orbigny 1835	high	both	Wilhelm 1951 <sup>5)</sup> , Ehrhardt 1991 <sup>4)</sup> , Markaida & Sosa-Nishizaki 2003 <sup>4)</sup> , Markaida 2006 <sup>4)</sup> , Markaida et al. 2008 <sup>4)</sup> , Ibáñez et al. 2008 <sup>3)</sup>
<i>Illex coindetii</i> Verany 1839	comm.	inter	Lordan et al. 1998 <sup>2)</sup>
<i>Illex illecebrosus</i> Lesueur 1821	comm.	both	Dawe 1988 <sup>4)</sup> , Dawe & Brodziak 1998 <sup>4)</sup>
<i>Illex argentinus</i> Castellanos 1960	comm.	inter	Bazzino & Quiñones 2001 <sup>4)</sup> , Santos & Haimovici 1997 <sup>2)</sup> , 2000 <sup>2)</sup> , Mouat et al. 2001 <sup>4)</sup>
<i>Martialia hyadesi</i> Rochebrune & Mabile 1889	incid.	inter	Rodhouse et al. 1992, González & Rodhouse 1998, Dickson et al. 2004 <sup>4)</sup>
<b>Family Loliginidae</b>			
<i>Sepioteuthis australis</i> Quoy & Gaimard 1832	comm.		Roper et al. 1984, Steer et al. 2003
<i>Uroteuthis duvauceli</i> d'Orbigny 1835	comm.		Roper et al. 1984
<i>Doryteuthis opalescens</i> Berry 1911	comm.		Roper et al. 1984
<i>Doryteuthis pealeii</i> Lesueur 1821	comm.		Roper et al. 1984, Maurer & Bowman 1985
<i>Loligo forbesi</i> Steenstrup 1856	comm.	inter	Roper et al. 1984, Rocha et al. 1994
<i>Loligo vulgaris</i> Lamarck 1798	comm.	inter	Roper et al. 1984, Sauer & Lipinski 1991, Rocha et al. 1994, Coelho et al. 1997 <sup>2)</sup>
<i>Loligo sanpaulensis</i> Brakoniecki 1984	comm.	both	Santos & Haimovici 1998?
<b>Family Onycoteuthidae</b>			
<i>Onykia (Moroteuthopsis) ingens</i> Smith 1881	comm.		Phillips et al. 2003 <sup>2)</sup>
<i>Onychoteuthis borealijaponica</i> Okada 1927	comm.		Roper et al. 1984
<b>Family Architeuthidae</b>			
<i>Architeuthis dux</i> Steenstrup 1857	incid.		Bolstad & O'Shea 2004 <sup>5)</sup>
<b>Order Octopodida</b>			
<b>Family Octopodidae</b>			
<i>Octopus vulgaris</i> Cuvier 1797	comm.	both	Guerra 1978 <sup>6)</sup> , Smith 2003 <sup>6)</sup> , Oosthuizen & Smale 2003 <sup>6)</sup>
<i>Octopus californicus</i> Berry 1911	incid.	inter	Hochberg 1997 <sup>6)</sup>
<i>Octopus bimaculatus</i> Verrill 1883	incid.	intra	Ambrose 1984 <sup>6)</sup>
<i>Octopus briareus</i> Robson 1929	comm.	inter	Roper et al. 1984
<i>Octopus maorum</i> Hutton 1880	high	both	Grubert et al. 1999 <sup>6)</sup> , Anderson 1999 <sup>6)</sup>
<i>Octopus mimus</i> Gould 1852	incid.		Cortez et al. 1995 <sup>6)</sup>
<i>Octopus tehuilchus</i> d'Orbigny 1834	high	inter	Ré & Gómez-Simes 1992 <sup>6)</sup>
<i>Eledone massyae</i> Voss 1964	incid.		Ré 1998 <sup>6)</sup>
<i>Enteroctopus megalocyathus</i> Gould 1852	high	both	Ibáñez & Chong 2008 <sup>6)</sup>

<sup>1)</sup> direct observation, <sup>2)</sup> trawls, <sup>3)</sup> several methods, <sup>4)</sup> jig, <sup>5)</sup> stranded specimens, <sup>6)</sup> scuba.

cannibalism is sexual cannibalism where often the female devours the male (before, during, or after copulation) that in many cases is smaller than its female counterpart (Polis 1981, Elgar 1992). The benefits of this type of cannibalism are especially pronounced when two basic preconditions are met: (1) the females' fecundity increases with size or rather weight and (2) for the males' it is unlikely that they have more opportunities to mate (Johns & Maxwell 1997). As cannibalism often is associated with an asymmetry between cannibal and victim, sexual cannibalism could be more common in animals with strong sexual dimorphism in size (Elgar & Crespi 1992).

In cephalopods, the taxonomic group of interest of the present review, both preconditions are met: fecundity is size-coupled and most species are monocyclic, i.e. senescence and rapid death strike after the first reproductive season. Even semelparity is common among cephalopods (Rocha et al. 2001). This and a number of other specific life history traits found in most cephalopod species make cannibalism especially beneficial for this taxon. They show high growth and metabolic rates (e.g. Rodhouse & Nigmatullin 1996, Boyle & Rodhouse 2005) and all living coleoid cephalopods (i.e. all modern cephalopods with the exception of the Nautilidae) are voracious carnivorous that consume a wide variety of available prey (Boyle & Rodhouse 2005). Cannibalism has been reported for many cephalopod groups of both octopus and squids like e.g. such of the genus *Illex*, *Octopus*, *Sepia*, *Dosidicus*, *Onychoteuthis*, *Todarodes*, *Ommastrephes* and *Loligo* (Caddy 1983, Roper et al. 1984, Hanlon & Messenger 1996, Boyle & Rodhouse 2005).

With the exception of a short section in Hanlon & Messenger (1996) and Boyle & Rodhouse (2005), a review on the subject does not exist and the effects of cannibalism on individual cephalopods and their populations are unknown. The present article reviews the available literature on cephalopod cannibalism to explore the patterns of different cannibal species and possible causes for it. It examines population densities, mating seasons, food shortages and the hierarchies of body size and between sexes, which all can be relevant factors in the cannibalistic strategies of cephalopods or be related to it. Publications on the diet of 34 species of cephalopods cannibals were reviewed. The reported cannibalism was ranked in three arbitrary categories: (1) incidental with cannibalistic proportion of less than 1% of the diet, (2) common cannibalism with 1 to 10% of the diet, and (3) high with more than 10% of cannibalistic diet (Table IV-4). Where information was available cannibalism was classified into intra-cohort and inter-cohort predation of

conspecifics. Further separation of the observed cannibalism considering biological and ecological reasons were made when possible.

### 4.3 - Generalized patterns in cephalopod cannibalism

All cephalopods are carnivorous and they have probably been active predators since their appearance in the late Cambrian as very early cephalopod fossils reveal (Boyle & Rodhouse 2005). This is one reason why the majority of the cephalopods are cannibalistic. We found 34 cannibal species of cephalopods in the literature, where 32.4% correspond to the family Ommastrephidae, 26.5% to the Octopodidae, 20.6% to the Loliginidae, 8.8% to the Sepiidae, 5.9% to the Onychoteuthidae, 2.9% to the Nautilidae and 2.9 % to the Architeuthidae (Table IV-4). In these 34 species cannibalism is incidental in 17.6%, common in 58.8% and high in 23.6 %. This pattern is unusual in animal kingdom and could be related to their voracious feeding behaviour, high metabolic demands, high abundances, and the absence of social behaviour.

**Table IV-5 Frequency of occurrence of cannibalism in the diet of *Dosidicus gigas* in relation to method of capture.**

Cannibalism [%]	Sampling gear	Location	Year	Reference
5 – 30	jigging	North Pacific	1980	Ehrhardt 1991
1.3 – 26.3	jigging	North Pacific	1995 – 1997	Markaida & Sosa-Nishizaki 2003
0.3 – 22	jigging	North Pacific	1998 – 2000	Markaida 2006
29.7 – 58	jigging	North Pacific	2005 – 2007	Markaida et al. 2008
3.7 – 7.1	jigging	South Pacific	1993 – 1994	Chong et al. 2005
7.8	purse-seine	South Pacific	2003 – 2004	Ibáñez et al. 2008
34.3	mid-trawl	South Pacific	2003	Ibáñez et al. 2008
3.3	trawl	South Pacific	2006	Ibáñez et al. 2008
28.9	jigging	South Pacific	2006	Ibáñez et al. 2008

In case of the squids, cannibalism in parts was thought to be the result of stress rather than a result of feeding habits only (Ibáñez et al. 2008) and such stress-induced cannibalism has been described for a number of species during fishing operations (Hanlon & Messenger 1996, Markaida & Sosa-Nishizaki 2003). Starving experiments on *Illex illecebrosus* in captivity where cannibalism was provoked after about three days corroborate the view of stress-induced conspecific predation (O 'Dor & Dawe 1998). Therefore, cannibalistic rates reported for commercial species of squids must be analysed with caution. Fishing inflicts stress and observed cannibalism or at least its intensity may be an artefact rather

than real data (Table IV-4). An extreme example is *Dosidicus gigas*, a nerito-oceanic squid where high rates of cannibalism were observed (Ehrhardt 1991, Markaida & Sosa-Nishizaki 2003, Markaida 2006, Markaida et al. 2008, Ibáñez et al. 2008). Cannibalism in this species showed temporal variations related to migration and in relationship of body size (Ehrhardt 1991, Markaida & Sosa-Nishizaki 2003). Additionally, fishing gear produces an artifact with respect to diet and the rate of cannibalism. Squids captured with jigs showed high cannibalism, while squids capture with nets usually were less cannibalistic (Table IV-5). The observed bias is thought to be related with 1) the predation opportunity and 2) the predator density. In northern Chile in years of poor abundance of *D. gigas* (usually warmer periods) its cannibalistic rate is very low (Table IV-5). For octopus species such bias due to sample gear does not exist as octopus is solitary and is usually taken one by one.

#### 4.4 - Effects of cannibalism on population dynamics

Years of high density of the schooling squid *Illex illecebrosus* were associated with high rates of cannibalism suggesting density-dependent relationships (Dawe 1988). In contrast, the populations of *Loligo sanpaulensis* that do not form dense aggregations show low incidence of cannibalism (Santos & Haimovici 1998). Cannibalism has been observed for jumbo squid (*Dosidicus gigas*) in years of mass strandings when its populations are forming large aggregations (Wilhelm 1951). Ommastrephid squids in general, show major abundance pulses related to interannual variations in environmental conditions (Anderson & Rodhouse 2001) and during episodes of high abundances population density cannibalism could be a regulating factor to reduce intra-specific competition.

When population density increases in case of octopuses (e.g. *Octopus briareus*) the territories must become smaller and subsequently the frequency of intra-specific encounters and the per capita rate of cannibalism increase (Aronson 1986). Similarly, for the octopus *Enteroctopus megalocyathus* and *Octopus vulgaris* a higher frequency of cannibalism has been reported in areas and periods where this species are more abundant (Chong et al. 2001, Oosthuizen & Smale 2003, Ibáñez & Chong 2008). Such situations theoretically generate a pattern in the structure of population sizes and/or impact stability of population cycles (Claessen et al. 2004). During El Niño-events the abundance of *Octopus mimus* increases in northern Chile which reflects in the catches (Castilla & Camus 1992, Defeo & Castilla 1998). This may provoke cannibalistic behaviour as a strategy of population

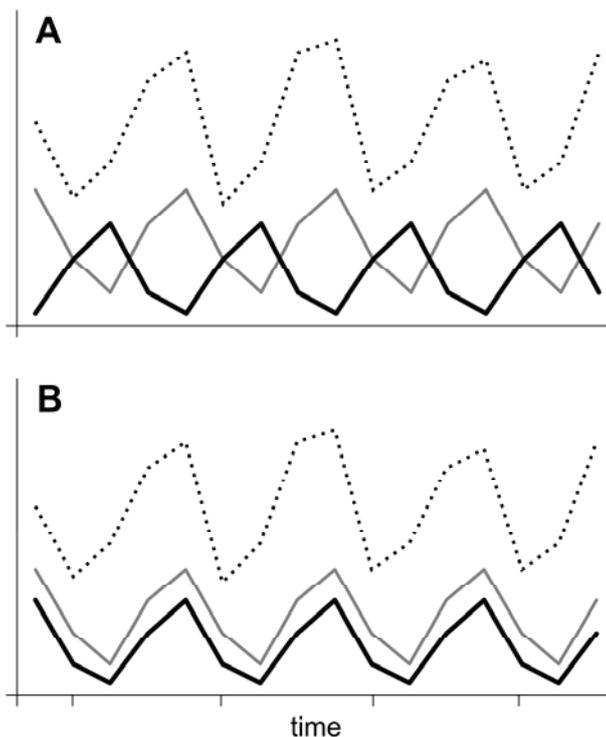
regulation that can stabilize population cycles (Claessen et al. 2004). However, in these periods high densities of bivalves, the main food of *O. mimus* (Cortez et al. 1995), were also found (Castilla & Camus 1992) which could keep the rate of cannibalism low.

It is assumed that cannibalism in case of cephalopods in general occurs mostly in populations with high densities. There the probability of conspecific encounters is elevated and the consumption of a member of the same species is more likely. However, it is difficult to conclude on this topic due to the limited number of studies and the fact of a bias due to sampling gear in case of squids (Table IV-4). Fluctuations in populations are the product of a number of factors that are either density-dependent or density-independent, and therefore it is of little value to test the existence of one type of factors exclusively (Lima 1995). Cannibalism could be a strategy of population regulation that leads to temporal fluctuations of this population (Fernández 1999, Claessen et al. 2004). Thus, the impact of cannibalism on population dynamics can be studied by comparing populations excluding cannibalism to population dynamics that result from different levels of cannibalism (Claessen et al. 2002).

The consideration of seasonal changes that occur especially in temperate environments can help to understand the mechanisms by which cannibalism can regulate a population in terms of productivity. The biomass of a population is determined by the carrying capacity of its ecosystem and the cannibalistic rate, the carrying capacity again is influenced by the varying productivity. In the months of increasing productivity a population of pelagic squids will increase its biomass. When productivity of the ecosystem declines the starving individuals increasingly feed on conspecifics that consequently decreases the biomass and results in population cycles (Figure IV-26A). In summary, squids are cannibalistic when the food is scarce and the population abundance is high. Cannibalism in this case acts density-dependent and occurs with a lag to the productivity of the ecosystem, i.e. in the example highest cannibalistic rate would occur in autumn/winter.

Squids living in shoals or groups have to be distinguished from the solitary and territorial octopuses as the different lifestyles lead to different types of intra-specific interactions. In case of the benthic octopuses, periods with increasing productivity will lead to increasing biomass and an increasing rate of encounters between conspecifics. This will lead to more aggressive behaviour producing a higher percentage of cannibals due to territoriality. As a

result biomass will decrease immediately leading to population cycles different from those of squids (Figure IV-26B). Here, cannibalism shows no lag to the environmental conditions and highest cannibalistic rate occurs in the period of highest productivity. It is assumed that inter-annual environmental variability, like e.g. observed during El Niño-phenomena or the cool and warm regimes in the Eastern Pacific, can have similar effect on the cannibalistic rates as seasonal changes of productivity.



*Figure IV-26 Effects of cannibalism and productivity on population biomass over three years. A) pelagic squids, B) benthic octopuses, dashed lines: productivity of ecosystem, black lines: rate of cannibalism, grey lines: squid/octopus biomass.*

A modelling approach on the general effects of mortality on population dynamics showed that during periods of reduced carrying capacity an extreme population reduction can be prevented by a rapid increase of mortality or a strong mortality pulse at or shortly after the appearance of adverse conditions. The abundance of a population then can persist at higher levels than without the increased initial mortality (Hallett et al. 2004), i.e. the increased mortality stabilizes the population level. Cannibalism could be such a mechanism that provides the necessary mortality to stabilize a population during adverse conditions.

#### **4.5 - Cannibalism as a strategy when food is scarce**

Cannibalistic behaviour has been suggested to be an indicator for limited food availability (Dawe 1988, Calow 1998). Ommastrephids and other squids are cannibalistic when they

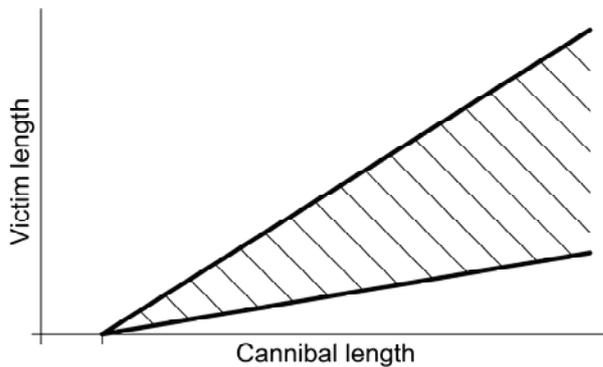
migrate in schools (O'Dor & Wells 1987, Rodhouse & Nigmatullin 1996, Mouat et al. 2001) and when food is scarce (Ennis & Collins 1979, O'Dor & Wells 1987). Cannibalism under such conditions can provide a mechanism for survival of at least parts of a school (O'Dor & Wells 1987) as it reduces competition for the limited resources and increases per capita consumption (Polis 1981, Calow 1998). Additionally, it can increase the ecosystem's carrying capacity (Polis 1981) by the indirect extension of the food size spectrum (Fox 1975). Larger specimens can access lower trophic levels when feeding on smaller conspecifics as shown in a population model for squids (Amaratunga 1983). This decreases the mean trophic level of the population and in that way makes it more efficient. Carrying capacity increases as does the survival rate of the larger individuals under otherwise insufficiently productive environments and secures reproduction (Keyl et al. 2008). Cannibalism in this sense has been coined life boat mechanism (van den Bosch et al. 1988, van den Bosch & Gabriel 1997). It has been assumed that cannibalistic populations in such situations could apparently even grow since the selective removal of small individuals leads to an increase in average weight of the population even without individual growth. A starving population with a high cannibalistic rate could seem to grow faster than one that is able to keep up a moderate consumption (O'Dor & Dawe 1998).

In *Illex illecebrosus* cannibalism was not related to abundance and probably occurs according to the availability of prey only (Maurer & Bowman 1985). Moreover, no significant differences in cannibalism of the squid *I. argentinus* for different size classes exist (Bazzino & Quiñones 2001) suggesting that in the study area food was sufficiently available. In loliginid squids cannibalism generally has been associated with limited food resources (Santos & Haimovici 1998). Cannibalism in *Loligo vulgaris* of the Saharan Bank is related to the high abundance of juveniles that constitute an alternative prey when other food is scarce (Coelho et al. 1997). In years of food shortages higher cannibalistic behaviour were observed also for *I. illecebrosus* (Maurer & Bowman 1985) and *I. argentinus* (Santos & Haimovici 1997). In the Gulf of California, cannibalism of *Dosidicus gigas* can raise to over 30% of the diet in months of prey scarcity (Ehrhardt 1991). Under adverse environmental conditions where primary productivity is reduced, the rate of cannibalism of cephalopods is likely to increase with the consequence of decreasing biomasses due to the elevated level of cannibalism (Pecl & Jackson 2007).

#### 4.6 - Inter-cohort cannibalism

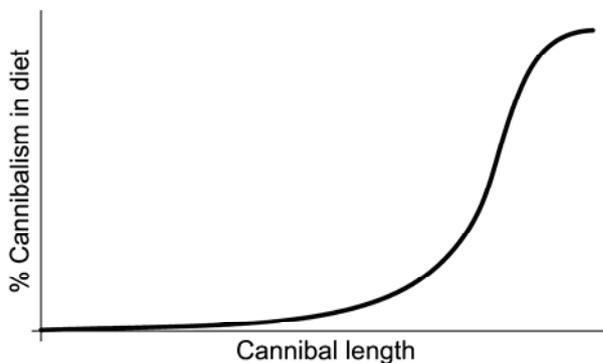
Adult cannibalism on juveniles is documented for several species of squid (Amaratunga 1983, Dawe 1988, Lipinski & Linkowski 1988, Sauer & Lipinski 1991, Rocha et al. 1994, Rasero et al. 1996, Santos & Haimovici 1997, Dawe & Brodziak 1998, Mouat et al. 2001, Markaida & Sosa-Nishizaki 2003) and octopus (Ré & Gómez-Simes 1992, Cortez et al. 1995, Anderson 1999, Grubert et al. 1999, Ibáñez & Chong 2008). Generally, cephalopods go through dietary changes of cephalopods during their ontogeny (Amaratunga 1983, Summers 1983, Rocha et al. 1994, Nigmatullin & Rodhouse 1996, Zuyev et al. 2002). From a crustacean diet during paralarvae and juvenile stages they switch to a diet consisting mostly of fish and cephalopods in their adult stage (Rocha et al. 1994). In teleosts the ontogenic change from planktivorous to piscivorous was suggested to be the result of the interplay between size-dependent competition and cannibalism (Claessen et al. 2000). Physiological and behavioural restrictions make cannibalism inherently dependent on the size of the victim and the cannibal (Claessen et al. 2000), increasing with age and depending on the size relation between both (Crowley & Hopper 1994, Claessen et al. 2000). In case of squids the results of a population model lead to the conclusion that cannibalism increases with age and promotes the transfer of energy from small individuals to larger ones (Amaratunga (1983).

Cannibalism is so common in adult squids that it was assumed that they are unable to maintain their daily consumption without a cannibalistic part in their diet, due to their high metabolic rates (O 'Dor & Wells 1987). Juveniles and sub-adults of *Illex argentinus* (<20 cm) also consumed conspecifics of 19% to 70% of their own mantle length but the highest frequency of cannibalism occurred among individuals of sizes larger than 20 cm ML (Santos & Haimovici 1997). Mouat et al. (2001) found that cannibalism in *I. argentinus* squid occurs only in case of large specimens and tends to increase with increasing squid weight. The frequency of cannibalistic specimens of *Dosidicus gigas* increases with size and a significant positive relationship between the size of the cannibal and the victim is reported for this species (Markaida & Sosa-Nishizaki 2003). *Todaropsis eblanae*, an ommastrephid cephalopod shows high incidence of cannibalism in an area of high density of juveniles (Rasero et al. 1996) and similar behaviour is known for teleosts as e.g. *Gadus morhua*, *Theragra chalcogramma* and *Merluccius gayi gayi* (Uzars & Plishs 2000, Wespestad et al. 2000, Cubillos et al. 2003).



*Figure IV-27 Predation window, the relationship between cannibal length and victim length.*

As individuals of the first ontogenic stages do not have the physical dominance, i.e. the capacity to kill and consume a conspecific we propose that the relation between size of the victim and the predator is following a linear relationship and an upper and a lower size limit (Figure IV-27). The resulting predation window (shaded area in Figure IV-27) defines the size range of prey for a specifically-sized cannibal (Claessen et al. 2000, 2002) that in case of cephalopods must be bigger than that of e.g. fish. Cephalopods have the capacity to prey on both relatively small and large prey due to the skilfulness of their arms and tentacles as well as the possibility to shred their food with their beaks (see Rodhouse & Nigmatullin 1996, Boyle & Rodhouse 2005).



*Figure IV-28 Relationship between cannibal length and cannibalism proportion.*

As the cannibals increase in size the proportion of cannibalism in the diet is assumed to be related in a non-linear form. Increasing size range of accessible victims together with the size-related increase of energy requirements that additionally are augmented greatly during maturation are supposed to result in non-linear increase of the importance of cannibalism in the diet of the cephalopod cannibal (Figure IV-28). Senescence at the end of a cephalopod's lifecycle (Anderson et al. 2002) as a consequence leads to lower energy intake of an individual and the here proposed sigmoid-like function. The cannibalism ob-

served during the last period of life is assumed to be primarily sexual (post-copulation) and in case of the octopuses additionally filial.

In *Octopus tehuelchus* cannibalism is important during the summer and autumn, when adults prey eggs and juveniles (Ré & Gómez-Simes 1992). A notable case of cannibalism is that of *O. maorum* in Tasmania, where cannibalism on small conspecifics and egg clusters (Anderson 1999) is second most important in the diet and has the highest weight percentage of all prey types (Grubert et al. 1999). Similarly, *Enteroctopus megalocyathus*, *O. tehuelchus*, *O. mimus* and *O. maorum* feed on their juveniles and females cannibalize their eggs (i.e. filial cannibalism) during brood care (Ré & Gómez-Simes 1992, Cortez et al. 1995, Grubert et al. 1999, Ibáñez & Chong 2008). It was assumed that the reason for the latter behaviour is that they eat nonviable or sick eggs to prevent further infections, as observed in *Bathypolypus arcticus* (Wood et al. 1998). In other taxonomic groups like fish, birds or mammals filial cannibalism is more common (Fox 1975, Polis 1981) and a high intake of eggs as e.g. reported for anchovy, can affect the recruitment of juveniles and cause inter-annual or intra-annual population fluctuations (Hunter & Kimbrell 1980, Pájaro et al. 2007). Due to the monocyclic life-history of most cephalopods this type of cannibalism in cephalopods only occurs in case of brood-caring species of octopuses and polycyclic nautilus (Arnold & Carlson 1986, Ré & Gómez-Simes 1992, Cortez et al. 1995, Wood et al. 1998, Grubert et al. 1999, Ibáñez & Chong 2008). It is not known how filial cannibalism affects the populations of species of these classes.

#### 4.7 - Intra-cohort cannibalism

Cannibalistic behaviour is affected by the sex of the cannibal and that of its victim as well as breeding related factors like e.g. the advance of reproductive season and individual stage of maturity. It has been observed that adult females of *Octopus cyanea* try to kill and feed on the male during courtship (Hanlon & Forsythe 2008) perhaps as a means of assessing the quality of the male (Elgar 1992, Calow 1998). *Sepia officinalis* shows cannibalistic behaviour only during the breeding season and associated with fights during mating (Pinczon du Sel et al. 2000) and cannibalism in case of *Loligo sanpaulensis* intensifies during mating in summer and fall especially at night (Andrighetto 1989). In *Illex argentinus* it intensifies in adults during autumn, the pre-reproductive period (Korokiewicz 1980, 1986). Cannibalism in general was thought to be a phenomenon associated with the concentration of squids in the spawning areas (Karpov & Caillet 1978,

Ré 1998). In case of *Illex illecebrosus* an alimentary hierarchy and population control results from cannibalism as females usually reach larger sizes than the males (Dawe 1988, O'Dor & Dawe 1998). In octopuses similar consequences have been observed in the laboratory and field, since the female of *Octopus maorum* and *O. cyanea* attack males after mating and even cannibalize them (Anderson 1999, Forsythe & Hanlon 2008). Small males of *Octopus vulgaris* are vulnerable to cannibalism by large females under laboratory conditions and the same was observed in their natural habitat (Hanlon & Messenger 1996).

The squids *I. illecebrosus* and *Dosidicus gigas* show marked sexual dimorphism with the females being larger than their males (O 'Dor & Dawe 1998, Markaida & Sosa-Nishizaki 2001), a factor that can generate competitive hierarchies in cannibalistic behaviour, especially in mating season. In case of *D. gigas* cannibalism is intensified during reproductive period and consequently sex-ratios are changing, leading to a still higher dominance of females in the population (Markaida 2001, Ibáñez & Cubillos 2007, Ibanez et al. 2008). However, it was also proposed that changing sex-ratios could be a direct, phenotypic response to food availability in their ecosystems (Keyl et al. 2008, Tafur et al. subm to MEPS). In myopsid squids cannibalism occurs among males, while in oegopsid squids it is inflicted by the females over males. This corresponds to the observed sexual dimorphism of the two groups: while in myopsid squids males are larger than females, in oegopsid the females are larger (O' Dor 1998).

#### **4.8 - Other implications of cannibalism**

Cannibalism has significant behavioural consequence as it affects the benefits of sociality (Hamilton 1964, Fox 1975, Polis 1981, Calow 1998). Cannibalistic behaviour is often directed at non-related individuals as filial cannibalism and siblicide (i.e. to kill brothers and sisters often combined with feeding on them) may reduce inclusive the fitness of the cannibal and have important impacts on fitness and sociability (Hamilton 1964, Fox 1975, Smith & Reay 1991, Calow 1998, Thomas & Manica 2003). Recognition of familiarity in cephalopods is possible, but not certain (Boal 2006) and the possible lack of recognition could promote non hetero-cannibalism in cephalopods.

The existence of an individual storage organ of cephalopods is still discussed and the capacity of the digestive gland to store energy in the form of lipids was generally accepted.

However, a number of studies found no evidence for this (Semmens 1998, Moltschanivskyj and Semmens 2000, Semmens 2002, Ibáñez et al. 2005) or found that the lipid metabolism of cephalopods is restricted (e.g. Phillips et al. 2001, Phillips et al. 2002). For *Dosidicus gigas* populational energy storage was suggested (Keyl et al. 2008). This feature would enable the individuals of this species to shift energy storing from the individual to the population. During favourable conditions the population size would increase rapidly in numbers and individual size. The resulting biomass (i.e. the stored energy) could then be reduced again by cannibalism during unfavourable conditions ensuring the largest specimens (i.e. the reproductive part of the population) to survive. This strategy would allow avoiding locomotory penalty due to large individual storage organs (O'Dor 1998) and nevertheless provide provision during fast migration (Bakun & Csirke 1998). Similar behaviour was suggested for *Illex illecebrosus* (O'Dor 1998) and may be more generally applicable for all cephalopods that are lacking a storage organ. Advantages of cannibalism in this context are the high quality of the food and the fact that no energy is lost due to conversion of ingested proteins to storable substances (fat, lipids). Such conversion is known to lead to losses of over 30% of energy at least in case of ureotelic animals (Millward & Garlick 1976 in Wieser 1994).

All forms of cannibalism may increase the risk of infestation with parasites reducing their fitness (Polis 1981, Calow 1998) although the transmission of disease via cannibalism is thought to be rare in natural populations due to more effective alternative infection mechanisms (Rudolf & Antonovics 2007).

#### **4.9 - Discussion**

Generally, an individual of a cannibalistic species that is physically more dominant or belongs to a group that ensures its physical dominance will be the cannibal. In many cannibalistic taxa an asymmetry exists in age, size or life history between the cannibal and its victim that generates the higher vulnerability of the victim (Elgar & Crespi 1992, Crowley & Hopper 1994, Claessen et al. 2000, 2002) and this is also true in case of the cephalopods (e.g. Markaida & Sosa-Nishizaki 2003). The cannibalistic window of cephalopods is wider than e.g. in fish because their morphological adaptations to capture and kill prey – their arms, tentacles and beaks – increase the opportunities to find cannibalistic prey.

Cannibalism is not a rare and abnormal behaviour that is only found in highly stressed populations, but is a natural response to environmental factors and conditions (Fox 1975). Clearly there are advantages for cannibalistic individuals as e.g. reducing competition and access to food of high quality (Fox 1975, Polis 1981, Calow 1998). In contrast, disadvantages for cannibals also exist as it is more expensive to feed on less abundant prey and this also implies the elimination of individuals with a shared genotype (Polis 1981). Cannibalism has evolved in many different organisms – probably analogously – and therefore must have an evolutionary benefit, such as avoiding local extinction during resource scarcity (Bobisud 1976, Nishimura & Isoda 2004). Population regulation by cannibalism must base on the process of group selection which can be inefficient compared to individual selection even when food is scarce (Reed & Stenseth 1984). Adopting cannibalism for a population could convert to a mutant strategy in the context of evolutionarily stable strategies (ESS, Maynard-Smith 1982, Reed & Stenseth 1984). As cannibalism implies a high risk of reprisals by the victims it was assumed that cannibalism cannot be an ESS (Dawkins 1976) but considering that it is an asymmetric interaction it might be an ESS nevertheless (Smith & Reay 1991). It may have a genetic origin, since the occurrence of several adaptations that inhibit or promote cannibalism implies the presence of selection on genes that may regulate the expression (Fox 1975, Polis 1981) but no studies exist for cephalopods in this respect. However, not all types of cannibalism need to be adaptive and the product of natural selection. Cannibalistic behaviour is described as response to stress, accidents and variable feeding behaviour related to changing environmental conditions (Polis 1981) and all these factors have been assumed to be possible factors controlling cannibalism in cephalopods (e.g. Dawe 1988, Markaida & Sosa-Nishizaki 2003, Ibáñez et al. 2008).

The stabilizing effect of cannibalism on population dynamics has been found for many species (see examples in: Fox 1975, Polis 1981) and the underlying mechanism is supposed to be related to the inflicted mortality (e.g. van den Bosch & Gabriel 1997, Hallet et al. 2004). However, destabilizing effects are also possible (e.g. van den Bosch & Gabriel 1997, Claessen et al. 2004) dependent of the ecology and behaviour of a species. Although we assume that among cephalopod species it is more common that cannibalistic behaviour stabilizes population level further investigations would have to be conducted to conclude on this topic.

In summary, to study cannibalism in cephalopods – as in other taxa – possible environmental variations as well as population density, food availability, body size and sexual dimorphism must be considered. It is very important to work with time series and/or simulations that can incorporate different rates of cannibalism and variable environmental conditions. Furthermore, laboratory experiments should be conducted to study the behaviour of the cannibals in relation to the variables mentioned. Future research on cannibalism must be oriented on five points:

- 1) Sampling should be carried out with different gear to avoid biases on stomach contents especially when relying on samples from fisheries. Methods like stable isotope, heavy metal, and fatty acid signature analyses should be used where possible.
- 2) Cannibalism must be studied over longer periods to compare with environmental factors (e.g. temperature, primary productivity) and ecological factors (e.g. abundance, food availability).
- 3) The asymmetry in size between cannibal and their victim must be explored by the search of cannibalistic window in an intra-cohort and inter-cohort approach.
- 4) DNA fingerprinting on victims from stomach contents should be employed to understand the role of sexual and filial cannibalism and if the cephalopod cannibal is able to recognize closely related member.
- 5) In an evolutionary context the origin of cannibalism in cephalopods must be identified by mapping cannibalistic and non cannibalistic species on phylogenies.

***Acknowledgments*** CI was supported by a CONICYT doctoral fellowship; FK thanks the colleagues of IMARPE for their kind support.



## CHAPTER V: Synopsis & Outlook

### 1 - Trait plasticity and energetic optimization as response to environmental variability: the case of the jumbo squid

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**Manuscript in preparation for submission**

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Keyl F, Yamashiro C, Ibáñez C, Argüelles J, Tafur R, Wolff M (in prep) Trait plasticity and energetic optimization as response to environmental variability: the case of the jumbo squid.

## 1.1 - Abstract

Cephalopods are especially plastic in their response to environmental variability and a number of factors like water temperature and food availability have been considered to be important for abundance, growth, size-at-maturity, fecundity and other morphological and life history traits. Jumbo squid (*Dosidicus gigas*) an ommastrephid cephalopod of the Eastern Pacific Ocean is an important ecosystem component and fishery resource that shows extreme plasticity in its response to ecosystem variability. Here we show that the changes of morphological and life history traits of *D. gigas* in response to environmental variability is marked and independent of fishery impact. Observed changes in biological traits follow an energy optimization strategy that allows the species to adjust to changing availability of prey and either emphasizes in survival of the population or the increase of individual fitness. The decoupling of maturation processes of the two sexes and the population energy storage basing on cannibalism further optimize the use of energy. Results are interpreted under the assumption of the hypothesis on size-defined, discrete sub-populations of Nesis (1970, 1983). Plasticity and the underlying energy optimization strategy are especially pronounced in jumbo squid but certainly not unique. Our results can help to identify similar schemes of biological traits in other marine species.

## 1.2 - Introduction

Organisms change their ecological, morphological and life history traits in relation to stimuli from the variable environment. This capacity to respond to changing intensities of environmental factors is found in many species of terrestrial and marine ecosystems (MacIntyre & Hutchings 2003). It is the inherent phenotypic plasticity of an organism if it does not involve a change of the genotype in contrast to genotypic plasticity that is based on different genotypes (e.g. Hoffman & Woods 2001, Price et al. 2003, West-Eberhard 2006). Two types of phenotypic response are distinguished. The first is continuous, that is a range of exogenous influences provoke a gradual change in the phenotype. It is also called the norm of reaction (West-Eberhard 2008). The second is polyphenism, where a discontinuous response function of the genotype expression to the environment leads to distinct, clearly separated phenotypes (Miura 2005). This form of plasticity is e.g. found in social insects where the genotype of all specimens contains the information for the development of all castes (Emlen & Nijhout 2000, Miura 2005). Both types of phenotypic plasticity can occur at the same time. A third type of response to the variability of extrin-

sic factors involves the genotype, that is, phenotypically different sub-groups that evolved through genetic assimilation are favoured under distinct environmental conditions (Price 2006).

The jumbo squid (*Dosidicus gigas*) is a large pelagic cephalopod of the Eastern Pacific Ocean (EPO) that reaches mantle lengths (ML) of up to 1.5 m (Roper et al. 1984). Like other cephalopods it is fast growing and can reach ML of nearly 1 m in one to two and a half years (Argüelles et al. 2001, Markaida et al. 2004, Nevárez-Martínez et al. 2006, Keyl et al. subm. to MEPS) which leads to a rapid passage through the trophic levels of its ecosystems (Nigmatullin et al. 2001, Keyl et al. 2008). It is monocyclic and dies after its first reproductive season (Rocha et al. 2001). A complicated population structure with three overlapping groups of size-at-maturity has been assumed (Nesis 1970, 1983, Nigmatullin et al. 2001) that is approximately consistent with Bergmann's rule: while the small group occurs in the Eastern Tropical Pacific, the large one is limited to higher latitudes in both hemispheres and only the medium sized group was thought to be found throughout the entire distribution range. As origin of these groups both phenotypic plasticity and genetic adaptation (Nesis 1970, 1983) have been proposed. Although Nesis (1970) himself doubted at least the distinction between the medium and large group, the fundamental review of Nigmatullin et al. (2001) on *D. gigas* has republished this population structure and following publications have taken the three groups for granted. However, a number of studies have reported the temporally restricted occurrence of medium and large size-at-maturity in northern Peru (Argüelles et al. 2001, 2008, Tafur et al. 2001) and the Mexican Gulf of California (GoC, Markaida 2006, Bazzino et al. 2007).

Cephalopods in general (Boyle & Boletzky 1996, Pecl et al. 2004, Boyle & Rodhouse 2005, Pecl & Jackson 2008, Pierce et al. 2008) and *D. gigas* in particular (Zeidberg & Robison 2007, Field et al. 2007, Argüelles et al. 2008, Keyl et al. 2008) respond highly plastic in their biological traits to changing environmental conditions. A number of factors but especially temperature and food availability have been proposed to play an important role (Mangold 1987, Forsythe 1993, Keyl et al. 2008, Pecl & Jackson 2008). Observed changes in size-at-maturity of the monocyclicly reproducing jumbo squid *Dosidicus gigas* were hypothesized to be a temporal adjustment to a change of these two factors in their habitat (Keyl et al. 2008). Similarly, changes of other biological traits were found to be affected (Keyl et al. submitted, Tafur et al. submitted, see below).

In case of the relatively small number of well-studied marine species that are usually those that have a history of extensive exploitation, changes in population parameters like abundance and size-at-maturity have often been attributed to the impacts of fisheries or their interactions with environmental variability (Pauly et al. 1998, Hutchings 2004, Ballón et al. 2008, Stenseth & Rouyer 2008, Stenseth & Dunlop 2009, Darimont et al. 2009). Often such changes are assumed to have a non-reversible impact on the genotype (Ratner & Lande 2001, Olsen et al. 2004, Kuparinen & Merilä 2007). For *D. gigas* it has been hypothesized that small and large size-of-maturity are favouring population survival and individual fitness respectively (Keyl et al. 2008).

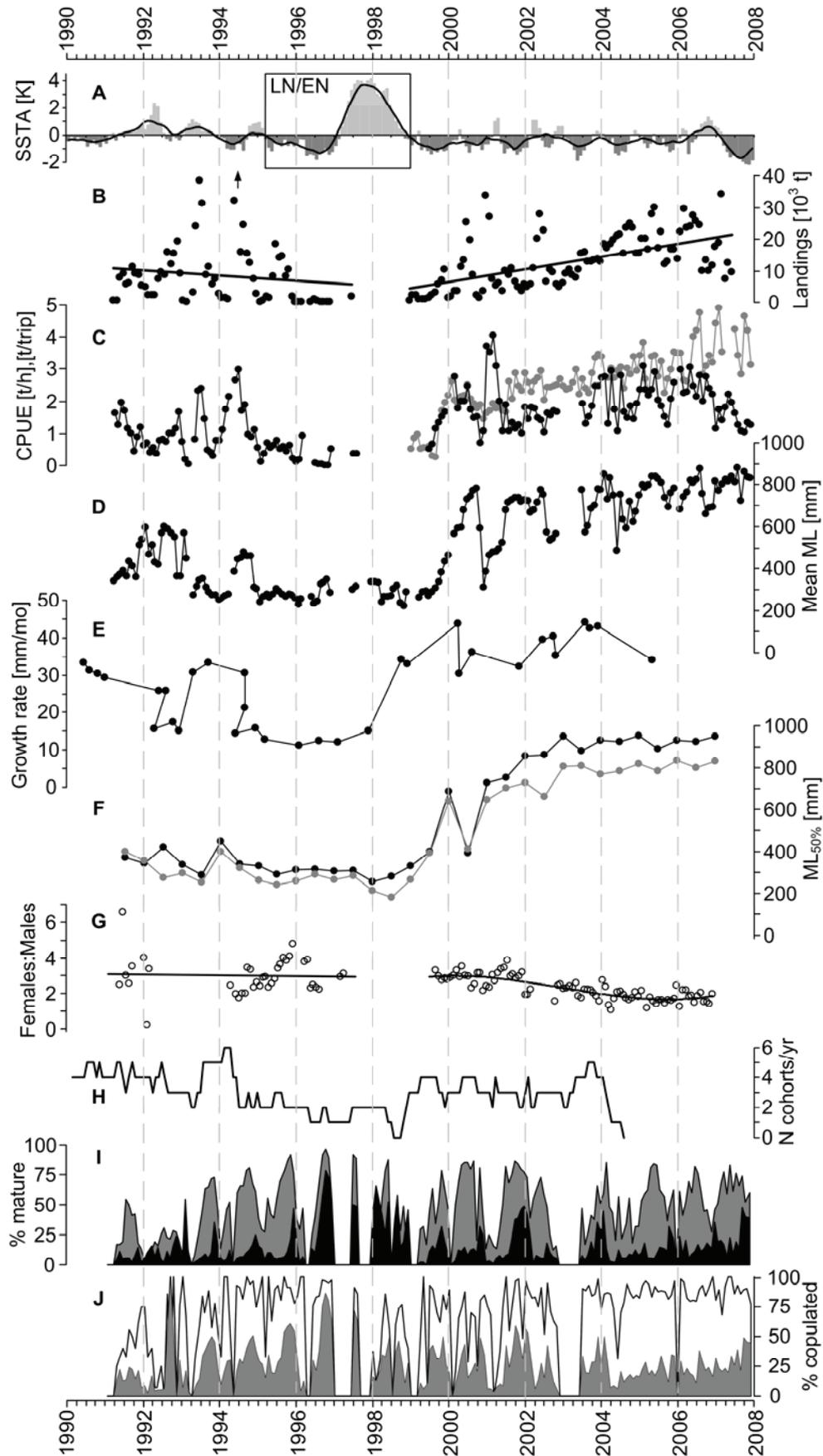
Here we analyse the variations of biological traits of *Dosidicus gigas* of the Peruvian Humboldt Current System (HCS) found in previous studies (Argüelles et al. 2008, Keyl et al. submitted, Tafur et al. submitted) together with new results in a holistic approach in relation to fisheries and the highly variable environment. The three groups of size-of-maturity of Nesis (1970, 1983) are also reviewed in this context.

### **1.3 - Material & Methods**

Methods for the analysis of the here presented results are described in Argüelles et al. (2008), Tafur et al. (subm.) and Keyl et al. (subm.). Data employed cover the period from 1991 to 2007 and were collected in the industrial fisheries in the Peruvian exclusive economic zone (EEZ). The biological dataset contains around 147,000 cases; the length-frequency dataset comprises over 4.3 Mio. cases. The fisheries dataset contains monthly information on landings and effort of the international industrial fisheries in the Peruvian EEZ and the two coastal artisanal fisheries in northern and southern Peru.

### **1.4 - Review of previous studies and results**

Morphological and life history traits of *Dosidicus gigas* are highly variable: results of previous studies and the present work found a marked shift after the strong EN 1997/1998 (Figure V-1A); a period in which jumbo squid has also expanded its distribution area (Zeidberg & Robison 2007, Field et al. 2007, Rodhouse 2008, Keyl et al. 2008). This coincides temporally with a regime of steadily increasing fisheries and growing abundance (Figure V-1B and C, IMARPE unpublished data). Catch per unit of effort (CPUE) is widely used as an index for abundance in exploited resources although limited in certain



**Figure V-1: Changes in morphological and life history traits, population abundance and structure compared to environmental conditions, (A) SST-anomalies of the Niño 1+2 monitoring box; (B) monthly landings of *D. gigas*; (C) abundance in the Peruvian EEZ as observed by industrial ([t/h], black line) and artisanal fisheries ([t/trip], grey line); (D) monthly mean size of landings of the industrial fishery [mm]; (E) growth rates (points plotted at estimated hatching dates of cohorts); (F) semestral size-of-maturity of females (black) and males (grey); (G) monthly female:male-ratio; (H) number of cohorts per year; (I) percentage of mature females (black) and males (grey); (J) percentage of copulated mature females (white) and all females (grey).**

aspects (Richards & Schnute 1986, Harley et al. 2001, Campbell 2004). Mean sizes of the landings increased at the same time (panel D, Figure V-1).

Growth rates of distinct cohorts identified by modal progression analysis showed to be highly variable with highest growth rates identified for cohorts that lived all or large parts of their life after 1998 (Keyl et al. *subm*, Figure V-1E). Simultaneously, mean size of mature females (Argüelles et al. 2008) and the size-at-maturity of both sexes increased in Peruvian waters (Tafur et al. *subm*, Figure V-1F). The female:male-ratio of *D. gigas* in the past was found to vary between 1:1 to 9:1 and more. In the Peruvian HCS in the 1990s sex-ratio has been fluctuating around 3:1 while after 2000 it slowly dropped to 2:1 (Tafur et al. *subm*, Figure V-1G). The number of cohorts per year has been found to be variable in the Gulf of California (Ehrhardt et al. 1983) and in the northern HCS. There the lowest number of cohorts was found from 1996 to 1998 during the strong LN/EN-sequence (Tafur et al. *subm*, Figure V-1H). The proportions of mature females and males as well as those of copulated females and mature copulated females until 2004 showed a more “peaky” behaviour as after that year when a change to a more “even” reproduction is observable (Tafur et al. *subm*, Figure V-1I and J).

The analysis of growth rates, maximum size and longevity of the cohorts identified by modal progression analysis (Keyl et al. *subm*.) suggest three different groups of cohorts (encircled in Figure V-2). Group one comprises the cohorts of the early 1990s and those of the 2000s, group two contains those that were hatched between mid 1994 and 1997 as well as three cohorts from 1992, and group three that encloses all other cohorts (mainly those of 1993/1994). Considering that these dates are the hatching dates, the cohorts of

the second group are those that run their life's course in the LN/EN-succession of 1996 to 1998 and the three cohorts from 1992 of that group can be associated to the 1992 EN (see

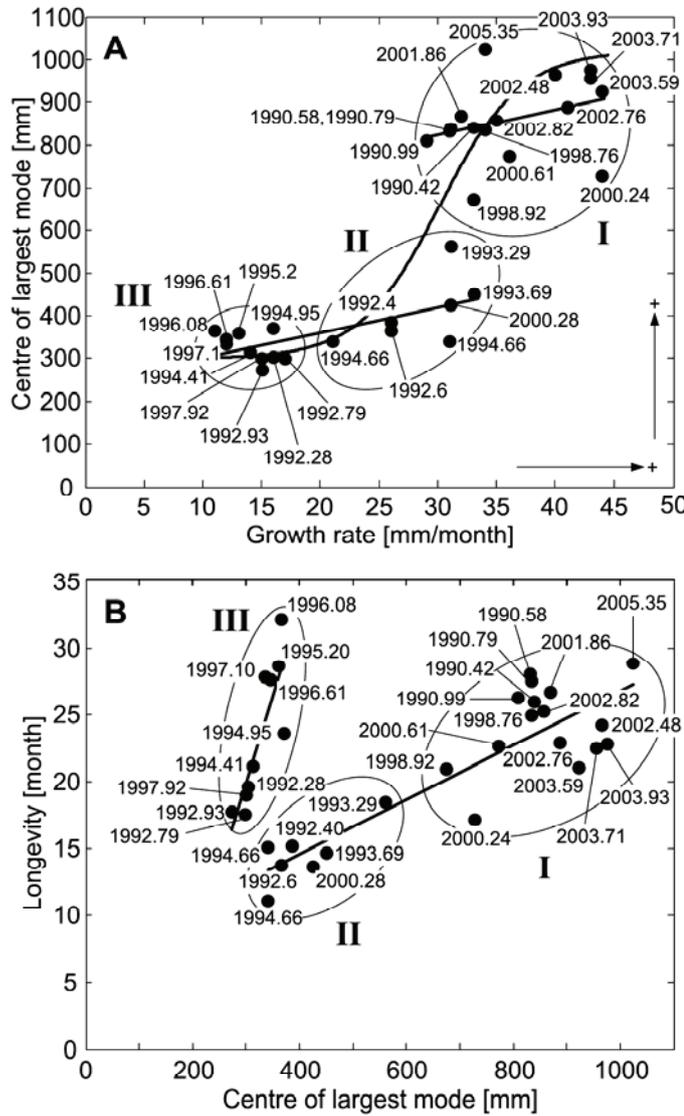


Figure V-2: A) relation between growth rate and maximum size of identified cohorts; arrows in the lower left corner indicate directions of increasing energy allocated to somatic growth; B) relation between longevity and maximum size of the identified cohorts; similar cohorts are encircled.

Figure V-1A and E). It can be observed clearly that terminal size of a cohort not necessarily is connected to longevity (Figure V-2B). Instead, two lineal functions ( $r^2 = 0.5280$ ,  $p = 0.06$  for group III of the LN/EN-periods and  $r^2 = 0.7206$ ,  $p < 0.01$  for the rest) are describing the relation between these two life history parameters. If one considers moreover that higher growth rates and larger terminal sizes have to be taken synonymous with higher energy requirements it can be assumed that the cohorts that are located close to the upper right corner of Figure V-2A are those that not only require most energy during their life but also have the highest energy uptake rate. Growth rate and maximum size of the

cohort lie between extremes that either may be seen as connected by a sigmoid function ( $r^2 = 0.7932$ ,  $p < 0.01$ ) or a discontinued linear function (discontinuity at 600 mm,  $r^2 = 0.93$ ,  $p < 0.01$ ). In the latter case groups II and III would belong to one group.

An analysis of gonadal length index (GLI) that relates the length of the gonads to mantle length showed that females mature in the last part of their life at or near their maximal sizes while males mature in the middle of their life and grow on to their maximal size afterwards (Tafur et al. subm.). Under the assumption of similar growth rates for females and males (Keyl et al. subm, but see Markaida et al. 2004) temporal decoupling of the maturation processes of the two sexes results. Immature females can be mated by males and store the spermatophores for later fertilization of their eggs (Nigmatullin & Markaida 2008). This leads to an extension of the reproduction period that gives *D. gigas* high reproductive flexibility and allows distributing additional energy requirements for reproduction over an extended period (Tafur et al. subm.). Percentage of copulated females correlates to that of mature males ( $r^2 = 0.34$ ,  $p < 0.01$ ) and corroborates the above findings.

## 1.5 - Discussion

Life history traits (i.e. size-at-maturity, sex-ration, reproduction and spawning time) and morphological traits (i.e. growth rate, longevity and maximal size) of marine species are influenced by changing environmental conditions and fishery. For marine resources often it has been assumed that especially fishing has severe and harmful impacts due to size-selective pressure (Rochet 1998, Coltman et al 2001, Hutchings & Baum 2005, Longhurst 2006, Jorgensen et al. 2007, Anderson et al. 2008). It has been found that environmental and fisheries impacts are difficult to distinguish (Ballón et al. 2008). During 1999/2000 a general shift has occurred in biological traits of *Dosidicus gigas* of the northern HCS that persists until present (Argüelles et al. 2008, Keyl et al. subm, Tafur et al. subm, Figure V-1) and may be attributed to the effects of fishery. However, we assume that the examined changes of traits were uniquely induced by environmental variability as they took place in the opposite direction as would be expected under an increasing fishing regime: mean size and size-at-maturity that are most often mentioned in this context suddenly rose and have been increasing further since.

Jumbo squid inhabits the highly variable neritic-oceanic waters of the Eastern Pacific Ocean. Like any other species to survive it needs to be capable to cope with the full range of environmental variables in its habitat. The observed changes of traits of morphology and life history (Tafur et al. *subm*, Keyl et al. *subm.*, present results) are assumed to give this ability. Due to basic biochemical principles well pronounced relationships between water temperatures and growth rates as well as reproductive processes could be assumed. Higher temperatures during EN-events should therefore lead to observable direct relationships between biological traits and sea surface temperature anomalies (SSTA; Pecl & Jackson 2008). Nevertheless, the observed variability of traits showed no such response to SSTA of the Niño 1+2-area that was assumed to reproduce environmental conditions of the northern HCS (all  $r^2 < 0.12$ , most  $r^2 < 0.06$ ). Apparently a more complex, possibly nonlinear link governs the interactions between the traits of jumbo squid and the environment.

Morphological and life history traits can be seen under the aspect of their energy demand (Brown et al. 2004) and in this context food availability must be an important factor for the energy demanding processes related to maturation (Mangold 1987). As jumbo squid is a monocyclic organism, energy available to *D. gigas* also regulates its terminal size. The observed variations of traits in the context of their energy demand are consistent: their states after 1999/2000 compared to those before this time are energetically elevated. This massive, uniform occurrence of trait changes after 1999/2000 leads to the assumption that *D. gigas* adjusts its morphological and life history traits to varying availability of prey under a holistic “energy optimization” strategy.

The female:male-ratio follows this pattern. Under the above assumptions, during periods of low food abundance a population is favoured when it can reduce the number of males that do not directly contribute to reproduction (Keyl et al. *subm*). Taking into consideration that mixed paternity is found in the batches of singles females (Nesis 1983, Hanlon et al 1999, Boyle & Rodhouse 2005) the effect on genetic variability must be less important as it may appear at first glance.

We assume that total energy available for an individual jumbo squid and its cohort and subsequently the form of appearance of their morphologic and life history traits reflects a “history of productivity” of habitats through which it migrated during life. Productivity in

the region is roughly related to temperature, and cooler water masses and especially the cold coastal upwelling waters (CCW) are energetically richer than warmer water masses. The CCW that by wind-induced Ekman processes are transported offshore enrichen a broad coastal band in the HCS (Calienes & Guillén 1981, Bertrand et al. 2004, Swartzman et al. 2008). The effects of climate oscillations change wind and current patterns and determine the distribution and locations of water masses in the HCS that finally influence the productivity of marine areas. Warm periods, but especially strong EN-events interrupt coastal upwelling (Morón 2000, Bertrand et al. 2004, Arntz et al. 2006, Graco et al. 2007) and lead to a reduction of the distribution area of the cool, productive waters. During cool periods, like LN, the opposite happens and the productive band of mixing waters widens due to intensified upwelling and the weakened EUC (Morón & Sarmiento 1999, Morón 2000, Graco et al. 2007, Keyl et al. 2008). As water masses are mainly defined by salinity and temperature, a stationary sample station of oceanographic variables or a climatic index indirectly can give hints on spatial processes of the system. In the present case the SSTA of the Niño 1+2-area allow basic predictions on the distribution and extension of water masses in the northern HCS. The negative state of the Niño 1+2-SSTA after 1999 can be interpreted as expansion of cool, productive water masses (Keyl et al. 2008) that lead to the expression of the energy-rich states of the traits of *D. gigas*.

The question then remains why the Niño 1+2-SSTA series does not correlate with the trait series (see above). Although we can only speculate on this here, apparently the link is not lineally reproduced by the SSTA and the picture is more complicated as it seems at first. After all, water masses are described only in parts by temperature and a number of factors determine the productivity of waters (Swartzman et al. 2008). It is thus certainly the case that waters with the same temperatures show different productivity. Additionally, it must not be forgotten that the Niño 1+2-area covers only parts of the northern HCS and the Peruvian EEZ where sampling was carried out.

Nearly all data used here were taken in the Peruvian exclusive economic zone (EEZ); they can not give testimony on the part of the population further offshore. However, a study analysing samples of the Chinese jigging vessels taken further offshore in austral winter of 2001 found size ranges and size-at-maturity of jumbo squid similar to the smaller cohorts during the mid to end 1990s (Ye & Chen 2007). This bimodal spatial distribution of sizes has been predicted (Keyl et al. 2008) and supports the here postulated

energy optimization scheme. The warmer, less productive subtropical surface waters (Bertrand et al. 2004, Swartzman et al. 2008) that during the mid-1990s were found inside the Peruvian EEZ after 1999 were displaced further offshore (Keyl et al. 2008).

Jumbo squid like most other cephalopods is living “in the fast lane” (Jackson & O’Dor 2001), that is, it is growing to large sizes in short time (Argüelles et al. 2001, Markaida et al. 2004, Keyl et al. *subm.*). Thus, its complete physiological and ecological processes must be setup to meet the resulting constant high energy demand. The here proposed “energy optimization” strategy with variable morphological and life history traits is one part to meet this demand. On the physiological level a number of features including protein-based metabolism, sustained growth, efficient handling of oxygen and reduced antioxidative defence were proposed that aid to realize the energy demanding “fast” life of squids (Jackson & O’Dor 2001). On the ecological level two basic mechanisms are developed in *D. gigas* that also support the overall energy optimization scheme. These not only reduce overall energy demand but also allow distributing it temporally to reduce the instantaneous rate of energy requirement and inter-sexual competition (Ibáñez & Keyl *in press*, Keyl et al. 2008, Tafur et al. *subm.*).

The first mechanism is the “population energy storage” (Keyl et al. 2008, Ibáñez & Keyl *in press*) that bases in high cannibalistic rates (Markaida & Sosa-Nishizaki 2003, Markaida 2006a, Keyl et al. 2008, Ibáñez et al. 2008) and enables *D. gigas* to shrink individual storage organs. The relative weight of the digestive gland, the only lipid containing structure in cephalopods, was found to be only 3.46% of total weight and with little variation ( $\pm 1.47\%$ ). In this way jumbo squid not only escapes the motility handicap associated to storage organs (Polis 1981, O’Dor 1998) but also the energy loss by conversion of ingested proteins to storage metabolites (Wieser 1994) and back. Instead energy is stored in the population as such by increasing its number during energy-rich conditions and reducing it if necessary by cannibalism during unfavourable states (Keyl et al. 2008, Ibáñez & Keyl *subm.*).

The second mechanism is the temporal decoupling of the maturation processes of the two sexes (Tafur et al. *subm.*). It allows distributing energy required for reproductive tissue and in this way reduces punctual energy demand and inter-sexual competition for resources. Together with the ability of females to store spermatophores even when imma-

ture (Nesis 1983), the decoupling expands the reproductive period of *D. gigas* (Tafur et al. *subm.*). Similar decoupling of female and male maturation has been found for other cephalopods (Forsythe 1993, O'Dor & Dawe 1998, Dunn 1999).

Plasticity of biological traits is always connected to costs and fitness (e.g. Price et al. 2003) and in the context of energy availability a trade off between population survival during adverse conditions and individual fitness and genetic variability during energy rich conditions was proposed by Keyl et al. (2008). The here proposed energy optimization strategy and the observed changes in traits corroborate this view at least for the small group. For the proposed increase of fitness of the large group no solid evidence can be given here. However, the occurrence of the lower female:male-ratio during the energetically rich 2000s is supporting the proposed connection to individual fitness. It also allows an increased genetic diversification of the population. Either a sigmoidal or a discontinuous linear function describes the relation between growth rates and maximal size of the identified cohorts and both similarly specify size extremes (Figure V-2A). In both cases the existence of the three delimited groups of size-at-maturity as proposed before (Nesis 1970, 1983, Nigmatullin et al. 2001) is doubtful at most. Nesis (1970) himself was uncertain with regard to the distinction of the two larger groups. After reviewing this work and catch methods here it is assumed that consecutive cohorts were mistaken for the proposed groups of size-at-maturity.

If understanding that increasing size and increasing growth rate result in higher absolute energy demand and per unit of time, it can be proposed that *D. gigas* has two growth related possibilities to respond to low energy conditions: to reduce size and to reduce growth rate. In mid-range of available energy of its ecosystem, supposedly related to "normal" or "optimal" environmental conditions, *D. gigas* responds by changing size and growth rates. If, after reaching its size extremes, energy content further increases or decreases, jumbo squid only responds by altering its growth rate (Figure V-1A) which can explain the intuitively confusing pattern of cohorts with small, but old specimens (Figure V-2B). Generally, the fact that large terminal sizes are reached only by these cohorts that also show high or very high growth rates (Figure V-2) supports the supposed dependency of the onset of maturation from food availability (Mangold 1987) that in case of the monocyclic *D. gigas* again governs maximal size. Similar dependence of the onset of

maturation from food availability is supposed to occur in other monocyclic cephalopod species as proposed by Mangold (1987) and others.

If considering the discontinuous linear function that obtains a better fit, the origin of the size differences is less clear. The response could either be the result of polyphenism (e.g. Miura 2005) or of two genotypes. Both options could explain the existence of the different groups of size-at-maturity although the existence of one discontinuity points to two size groups and not three as proposed Nesis (1970, 1983). The latter option of the origin of the groups must result in genetically different sub-populations. Generally, a number of reasons lead to a genetic assimilation of phenotype variation, that is, differences in genotype. In case where environmental variability is high, like it is found in the HCS, phenotypic plasticity as such may be favoured if it can respond sufficiently to the change (Price et al. 2003) and as a consequence result in an evolutionary stable strategy itself. In other words, in such environments the phenotypic plasticity is the adaptation and prevents further genetic assimilation to different environmental conditions that would result in different genotypes. We therefore assume that genetically different sub-groups do not exist. The fecundity of *D. gigas* (Nigmatullin & Markaida 2008) and its migratory behavior probably result in a true panmictic population. This supports the hypothesis of phenotypic plasticity as origin of size-groups as under such circumstances extreme selective pressure and spatial separation would have to be in effect to produce groups with different genotypes. In case of *D. gigas* even specimens of the two hemispheres show no or only little genetic diversity (Sandoval-Castellanos et al. 2007).

Although the proposed population structure of Nesis (1970, 1983) and a genetic origin for it seems unlikely, the results of this study do not allow concluding terminally over the subject. Further investigations, ideally of genetic nature, will have to be conducted to resolve the question of existence and origin of the groups of size-at-maturity proposed by Nesis (1970, 1983).

Here we propose an energy optimization scheme under which biological traits adjust to the energetic conditions of the ecosystem. The clear perceptibility of the plasticity of morphological and life traits as in the present example of *Dosidicus gigas* is uncommon but we assume that such directed trait plasticity cannot be unique in nature. Jumbo squid therefore may serve as a model that allows us to understand analogous, less visible

changes of traits in other species. Our results have implications for the management of *D. gigas* and may be considered in that of other exploited natural resources where changes of morphological and life history traits have been solely attributed to the impacts of fisheries. Not only must natural environmental oscillations be accounted for in the future but also alterations linked to the anthropogenic induced global change.

***Acknowledgements.*** We thank all our colleagues at the IMARPE that kindly supported and advanced our work with their knowledge, experience and advice, especially those from the Marine Invertebrate Department and all on-board observers.

## **2 - Environmental variability and fisheries: what can models do?**

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**Published in Reviews in Fish Biology and Fisheries**

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Keyl F, Wolff M (2008) Environmental Variability and Fisheries: What Can Models Do? Rev Fish Biol Fish 18:273-299

## 2.1 - Abstract

This review is based on 58 climate-fisheries models published over the last 28 years that describe the impacts of fishery pressure and environmental variability on populations and ecosystems and include basic principles of population dynamics. It points out that the incorporation of environmental factors in fishery models has already been done and is of great importance for future models used in the assessment of marine resources. The work is guided by the questions to what extent have these models (a) enhanced our understanding of the interrelationships between the environment, the fishery and the state of the exploited resources and (b) helped to improve the prediction of population dynamics and the assessment of marine resources. For each of the six most commonly used model categories a case study is critically analyzed. The problems of “breaking relationships” between environmental factors and the biological response used in models, the trade-off between model complexity (realism) and simplicity (data availability) and the potential of multivariate climate indices for forecasting ecosystem states and for use as proxies for combined models are discussed, as are novel non-linear and spatially explicit modelling approaches. Approaches differ in terms of model complexity, use of linear or non-linear equations, number of parameters, forecast time horizon and type of resource modelled. A majority of the models were constructed for fish and invertebrate stocks of the northeast Pacific and the epicontinental seas of the Atlantic, reflecting the advancement of fisheries science in these regions. New, in parts highly complex models and sophisticated approaches were identified. The reviewed studies demonstrate that the performance of fished stocks can better be described if environmental or climatic variability is incorporated into the fisheries models. We conclude that due to the already available knowledge, the greatly enhanced computer power, new methods and recent findings of large-scale climatic/oceanographic cycles, fisheries modelling should progress greatly in the coming years.

**Keywords:** Fishery models, Environmental variability, Climate oscillations, Population dynamics, Stock assessment

## 2.2 - Introduction

### **The current situation of fisheries and fishery science**

Fishing is an important social and economic activity in many countries, especially in the developing part of the world. The growing demand for marine products will lead to a continuous increase in the exploitation pressure on most marine resources. For about a century, fisheries science has tried to understand the processes governing the dynamics of fish stocks and to predict sustainable yield levels of exploited marine resources. To enhance understanding and provide a sound basis for management, a wide range of models have been developed for the assessment of marine resources estimating individual numbers or biomasses of populations subjected to different exploitation scenarios. Data used for these models comprise fishing effort and (reported) landings (total landings according to size and/or age groups) or data that – when economically feasible – were derived from scientific surveys. In spite of the great research effort devoted to fisheries assessment and management, the present state of the marine resources is alarming when considering the increasing demand on fisheries products: nearly one third of the resources are already overexploited and several commercial species are facing extinction. About the half of the world's marine resources are fully exploited (FAO 2007) and are currently in danger of being overfished. For the near future for mall stocks overexploitation is predicted (e.g. Pauly 2006, Worm et al. 2006) although this bleak picture of the future is questioned by others (e.g. Murawski et al. 2007, Jaenike 2007, Wilberg & Miller 2007). The present situation of the world fisheries is the result of the interplay of many different factors, of which economic forces, political interests, a lack of control and enforcement of fishery regulations, but also great natural variations of fish stock sizes and productivities and resulting poor catch predictions by fisheries models play a role (Quinn & Deriso 1999, Haddon 2001). While over the past century of fisheries science, a great number of biological, economic, social and environmental factors were considered in the construction of increasingly sophisticated models, catch predictions were only rarely becoming more successful.

Poor yield predictions and unexplainable natural stock fluctuations are often assumed to be the result of a variable environment that in most cases has just been considered as unpredictable “environmental noise” (Hilborn & Walters 1992, Quinn & Deriso 1999, Haddon 2001, Jonzén et al. 2001). The missing inclusion of this “noise” in fisheries

models has led to wrong estimations of the performance of exploited resources and as a result has contributed to the present deteriorated state of many marine stocks.

The questions raised by this review are to what extent the interplay of climate and fisheries has been understood over the past decades and what kind of promising modelling approaches have been developed that may guide future research in this field and that may be applied to the assessment of marine resources.

Research in ecological modelling has demonstrated that biological and ecological entities such as individuals, populations, communities and ecosystems and their trophodynamic interactions are influenced by their variable abiotic environment. Clear (and spurious) relationships and correlations were found between climatic, oceanographic and local environmental conditions. Different variables were identified that control the dynamics of the biological components of both marine and terrestrial systems (Hare & Mantua 2000). Variability of the biotic compartments induced by environmental variability (EV) has been found for all trophic levels, functional guilds and hierarchical levels of marine ecosystems (Bernal et al. 1983, Lluch-Belda et al. 1989, MacCall 1996, Boyd & Murray 2001, Lluch-Cota et al. 2001a, b, Chavez et al. 2003, Alheit & Ñiquen 2004, Ñiquen & Bouchon 2004, Iriarte & González 2004, Keyl 2004, Perry et al. 2004, 2005). It is well described that species not only respond in different ways to environmental changes but also populations of the same species do so in different localities (Skud 1982, Alheit and Bernal 1993, Francis et al. 1998; Hare and Mantua 2000, Alheit & Ñiquen 2004) as do the different age-classes of populations (Coulson et al. 2001, Ottersen et al. 2006). The population response to a change of intensity of a certain factor may even be into the opposite direction at different locations. Generally, it is assumed that the impact of EV is greater on the lower trophic levels (Francis et al. 1998).

Environmental and climatic variability (EV and CV) are closely interdependent. In the present review CV follows the definition of the Intergovernmental Panel on Climate Change (IPCC). Here, climate is understood as the “average weather”, i.e. the statistical description in terms of mean and variability of relevant variables (e.g. temperature, precipitation, wind) over a period of time that is classically assumed to be 30 years. In a wider sense, climate is the state of a climatic system (Houghton et al. 2001). Following this definition of climate of the IPCC, CV shall therefore refer to variations of this mean

state and other statistics on all temporal scales affecting this “average weather”. Local environmental conditions are the result of a mutual interaction of large-scale atmospheric and oceanographic conditions with the morphology in each geographical point. Environmental variability in the present review is therefore defined as the local variation of the mean state of the climate-dependent environmental conditions on a seasonal to geological timescale: Thus, the atmospheric and oceanographic conditions interacting with terrain morphology result in typical local environmental conditions with specific forcing factors affecting ecosystem entities and their trophodynamics.

Large-scale climate variability of the world’s ocean and atmosphere such as the ENSO-events El Niño and La Niña, which are characterized by significant changes of SST, sea level and other environmental conditions in the South-east Pacific over a period of several months, produces EV at various spatial and temporal scales that again influence the large scale variability (Paeth et al. 2003). As a result, a complex global system of interactions between CV and EV emerges with timeseries of local environmental variables that show significant local dynamics and nevertheless are often highly correlated to the large-scale CV (Hsieh et al. 2005).

Every model is being caught in the basic dilemma that only two of the aspects realism (the qualitative aspect), precision (the quantitative aspect) and generality (the aspect of the universality of applicability) can be satisfied with one approach (Levins 1966). If considering a specific system the problem is often reduced to the trade-off between realism and precision, which translates to the trade-off between the systematic and the statistical error with the former decreasing with model complexity and the latter increasing. The target of the modeller should thus be an intermediate level of complexity that allows grasping the main factors and processes to be described and still performs statistically well (Walters & Martell 2004). For assessment and management of marine resources a simple model has the great advantage of low data requirements and low statistical error but it may miss important processes of the system and as a consequence may result in overexploitation or underexploitation with high monetary loss. The construction of a more complex and realistic model on the other hand may be very data intensive and may produce a higher statistical error reducing its value for the application due to large confidence intervals (Walters & Martell 2004). The incorporation of environmental factors introduces more complexity due to a higher number of parameters and hence automati-

cally moves a model towards the direction of higher statistical error. This problem has to be considered when proposing such “combined models” for management, as the higher uncertainty will certainly constrain their application to some account as it has been the case with complex ecosystem-based approaches.

### **Brief look into the past**

The detection and quantification of variability in ecological timeseries has newly awakened the interest in research on the dependency of biological performance on abiotic factors as the growing body of publications of the last two decades shows. The importance of variability in the performance of biota was already found in the very beginning of life sciences. Van't Hoff, the Nobel Prize winner of 1901, formulated the Q10-rule and before him von Liebig (1855) had put forward the law of the minimum. Accordingly, animal populations may not be limited by the total amount of resources available throughout the year, but by the minimum amount of resources available to that population at the time of greatest scarcity. Blackman (1905) was the first to define exogenous factors, referring to the rate of photosynthesis as a function of light intensity, temperature and CO<sub>2</sub>-concentration. Fry (1971) classified limiting factors for fish growth and survival and gave upper and lower survival limits. From the early years of the twentieth century, fisheries scientists had already emphasized that economically important stocks were highly variable (Hjort 1914, Johansen 1925, Carruthers 1938, Rae 1957, Cushing 1982) due to the ever changing environmental conditions they are exposed to.

Nevertheless, EV was not further considered in the methodology used for assessment and management of marine resources since fisheries biologists and ecologists generally assumed it to be of stochastic nature (e.g. Ricker 1958, Hilborn & Walters 1992, Quinn & Deriso 1999, Haddon 2001). A prediction of future stock dynamics (and population size) considering the combined influence of both fisheries pressure and EV was considered rather impossible. A problem was also seen in the fact that the forecast potential of an environmental variable (such as temperature) was only possible at a much shorter time scale (days to seasons), than the available annual fisheries yield series.

While one type of model of the golden age of fishery science, Ricker's stock-recruitment relationship (1954, 1958) allows inclusion of environmental variability, it was most often applied without, and recruitment was just modelled as a function of spawning stock size

even though annual recruitment at a given stock size showed great variability (Koslow 1992). Further work in the field of combined modelling of the influences of fisheries and EV on population dynamics was and is considered by some fisheries scientists and resource managers to be not possible. In the following quote from Hilborn & Mangel (1997) this situation in fishery sciences is well reflected: “Since fishing pressure can be managed but the environment cannot, the default assumption in fisheries models has been to assume that the changes are due to fishing pressure. Thus, we use models without systematic environmental changes and leave the challenge of realistically considering environmental change for the next generation...” The general belief in a stochastically changing environment, which can just be considered as noise in the fishery models, went along with the paradigm of density-dependence of fish stocks (Krebs 2002), as postulated by the widely used Schaefer (1954, 1957) surplus production model. The idea of the dependence of ecosystems and their resources on the changing (abiotic) environment, although not forgotten, was more or less ignored, despite the occasional attempts of fisheries scientists to emphasize the importance of EV and CV in the dynamics of many fish stocks (e.g. Burkenroad 1948, Cushing 1982).

### **New perspectives for the incorporation of environmental and climate variability**

Advances in the field of climate forecasting and the prediction of oceanographic oscillations and patterns are mainly due to the rapidly developing computing power in the last few decades. It appears that the simple fact that a standard personal computer in 2006 has more computing power than a hall filling computing machine of earlier generations has rocketed insight into climatic and oceanographic systems' functioning as it has allowed for the use of new methods and models such as the complex general circulation models (GCM). The increasing length of available instrumental time series has enabled the identification of longer (i.e. decadal-scale) oscillations and the construction of large proximal variable timeseries of geological origin has provided the possibility to glance further into the past and to get a hint on these cycles in the distant past. Additionally, these long-time proximal series open the possibility to detect oscillations with durations of millennia and longer.

Synchronous changes of fishery yield of geographically separated populations, found for example in economically important clupeid fish stocks (Lluch-Belda et al. 1989,

Schwartzlose et al. 1999, Klyashtorin 1998, 2001, Chavez et al. 2003) or marine zooplankton (Perry et al. 2004) strongly indicate that fishery pressure alone cannot explain the observed synchronies. The governing factors according to the above authors must be linked by spatially large-scale atmospheric and oceanographic mechanisms. For the Humboldt Current large marine ecosystem (HCLME), off Peru and Chile, Alheit & Bernal (1993) postulate that supra-regional oscillations of climatic and oceanographic variables with different frequencies in addition to fishing pressure are responsible for the variability of marine resources observed in this ecosystem. This view is supported by fluctuations found for unexploited resources in the HCLME (Loeb & Rojas 1988, Muck 1989a, Ayón et al. 2004) and other places (Sugimoto & Tadokoro 1997, Hare & Mantua 2000, Beaugrand et al. 2002, Beaugrand & Reid 2003). The results of various analysis of geological proximal timeseries that were reconstructed from deposited scales of anchovy and sardines in marine sediment-cores off the Californian Pacific Coast and date back 1700 years are also consistent with this hypothesis: abundance crashes similar to the modern ones assigned to the influence of fisheries are found in the prehistoric past (Soutar & Isaacs 1969, 1974, Baumgarten et al. 1992, Dean & Kemp 2004). An archaeological investigation in Peru (Sandweiss et al. 2004) and the analysis of historical data of northern Europe (Alheit & Hagen 2002) further strengthens these findings.

Two features regarding climate and its variability have been becoming more and more confirmed and have opened the path to advances in ecological modelling: the existence of a global warming trend and the cycles of coupled climatic-oceanographic patterns documented in indices like the SOI (Southern Oscillation Index), PDO (Pacific Decadal Oscillation) or NAO (North Atlantic Oscillation) that capture the cyclic behaviour of the Pacific basin and the North Atlantic. These features influence the physical environment of – and the interactions within – the ecosystem; a great number of geomorphologic impacts have been described by Viles & Goudie (2003). Climate oscillations were retrieved not only from instrument-based indices as those already mentioned but also from timeseries of geological, prehistoric, historic, biological and economic origin (e.g. Soutar & Isaacs 1969, 1974, Lluich-Belda et al. 1989, Baumgartner et al. 1992, Klyashtorin 1998, Hare & Mantua 2000, Biondi et al. 2001, Sandweiss et al. 2004, Ourbak et al. 2006). The origin of climatic cycles is assumed to be found in the astronomic oscillations (Milanković cycle, sun spot cycle and others) and the deviations of these (Royer 1993, Parker et al. 1995, Lean 2002, Berger et al. 2002, Cobb et al. 2003, Cane 2005). The ecological and social

effects of decadal-scale climate and environmental fluctuations have been the object of various reviews of the last few years (Ottersen et al. 200, Smetacek et al. 2002, Stenseth et al. 2002, Walther et al. 2002, Chavez et al. 2003, Stenseth et al. 2003).

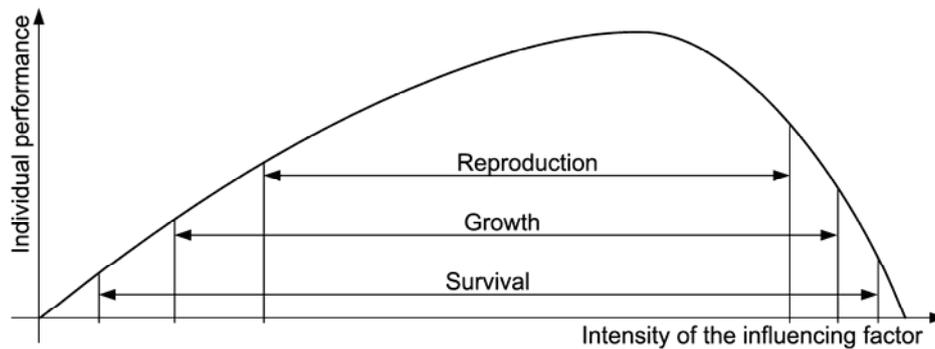
Various indices describing decadal scale oscillations like the PDO and the Interdecadal Pacific Oscillation (IPO) show a relatively marked flip-flop behaviour with two regimes (“cold” and “warm”) tipping over from one state to the other in a remarkably short time span of a few years or less. Other indices like the North Atlantic Oscillation or the globally important Arctic circulation index (ACI) have two less abrupt alternating modes. The decadal regime shifts were described by oceanographers and fisheries scientists who identified shifting states for many marine resources along the Pacific Rim of the North American continent (Wooster & Hollowed 1995, Mantua et al. 1997, Klyashtorin 1998, Hare & Mantua 2000, Hollowed et al. 2001, Mantua & Hare 2002). Long-term cycles and regime patterns described in the last decade for many climatic and oceanographic variables and their implications for local ecosystem conditions can open the way to design combined biological-environmental models able to predict future biomasses and fishery yields. Simple empirical sinusoidal models of climate indices were used in yield forecast models by Keyl (2004); similar sinusoidal models simulating landings timeseries of small pelagics according to Klyashtorin (1998, 2001) seem to give reasonable forecast periods of up to 60 years. Such an assumption certainly is questionable and oversimplified but the stable states (regimes) over a decade and more (deYoung et al. 2004) might give the possibility of an economical meaningful interannual predictability of global climate development. It is assumed that the decadal-scale frequency variability increases predictability possibilities (Mestas-Nuñez & Miller 2006).

At present the general nature and origin of the above stated and other climate oscillations as well as their predictability are controversially discussed. According to Hsieh et al. (2005) two opposing positions can be identified: one side – mainly physical oceanographers – supposes that the cyclic oscillations with regimes behaviour if existing are purely stochastic, originating in the red noise observed in many environmental time series (e.g. Wunsch 1999, Rudnick & Davis 2003, Solow & Beet 2005) while the other side – mostly biologists as the authors of the present review are – supposes that biological systems and entities respond in a nonlinear, amplifying manner to rapid environmental states and regime shifts of whatever nature (e.g. Mantua et al. 1997, Hare & Mantua 2000, Scheffer et

al. 2001, Overland et al. 2006). Aggravating is the fact that definitions are not always clear and that the terms regime and regime shifts are used by both sides although they possibly describe different phenomena creating irritation and misunderstanding (Overland et al. 2006). Some researchers state that the present statistical methods applied may not be sufficient “by themselves” to solve the problem (Steele 2004) or propose new methods to detect regime behaviour in climate timeseries (Rodionov & Overland 2005). Whatever in the end turns out to be the truth – the decision or even further argumentation is by far beyond the possibilities of the present review – we assume that by the use of relative simple models basing in the often observed cyclic nature of climate variability (examples in Overland et al. 2006) reasonable forecast results for the application in “combined” CV/EV-fishery models can be achieved. One general property of natural timeseries is their autocorrelation, i.e. the future to a certain extent is influenced by the present and past.

Models considering the dynamics of atmosphere and ocean, the general circulation models (GCM) are complex spatial explicit models that are able to not only capture the cyclic natural variability but also the trend for which global warming is held responsible for. A great number of this type of models exists simulating the physics of whole ocean basins to that of the entire globe with different underlying physical mechanisms. Although mostly spatially still too coarse in resolution to be directly used in CV/EV-fisheries models local EV timeseries can be correlated to their outputs. In the future resolution at least in specific areas is planned to become more detailed (Palmer et al. 2004) so that models used in resource assessment could be coupled directly to GCMs. The prediction time span equally is thought to increase (Latif et al. 2001); currently it is assumed that they have the skill to predict conditions of the oceanic environment from several months to decades ahead. Prediction of the sea surface temperature (SST) of the tropical pacific representing the El Niño-Southern Oscillation (ENSO) usually is made for around 9 months, but Anderson (2004) assumes the possibility of increasing the forecast span to 1 year with the model of Chen et al. (2004). The authors of the model themselves even suppose that a forecast of up to two years is possible with their model. Surface air temperature of tropical oceans according to Collins (2002) and Collins et al. (2006) are potentially predictable by GCMs on a seasonal to interannual level, those of midlatitudes of the North Atlantic on a decadal time scale. This forecast range of GCMs is consistent with the work of other scientists like Latif & Barnett (1996) or Palmer et al. (2004). The prediction of decadal

scale variability of SST is assumed to be possible “a few years ahead” (Venzke et al. 2000). Generally it seems that in the eastern Pacific predictability of the tropical realms is in the range of interannual level while that off the equator may be up to decadal-scale (Latif, IFM Geomar, personal communication).



**Figure V-3: Hypothetical biological response to changing intensities of an influencing factor with different ranges of performance of the individual (modified from Townsend et al. 2003)**

An earlier review article in Spanish by Wiff & Quiñones (2004) describes the environmental parameterization of fisheries models. The authors distinguished between three general types of models incorporating EV. The first comprises the theoretical-mechanistic inclusion of EV, the second the stochastic (random variation) method and the third type comprises those approaches using environmental timeseries. They and others (e.g. Hsieh et al. 2005) assume that most environment-ecosystem interactions are non-linear (see Figure V-3) or not even continuous as other researchers put forward (Scheffer et al. 2001, Collie et al. 2004) and therefore difficult to detect. It is proposed that one way to solve this problem is to empirically correlate biological or ecological factors to EV before progressing to models that include population dynamics. Due to temporally and spatially changing environmental conditions and to latitudinal or vertical gradients, the position of an ecosystem and its (often migrating) resources in space and time is of utmost importance for the modelling exercise (Cushing 1982, Muck 1989b, Lluch-Belda et al. 1989).

The present work reviewed 58 combined models of 48 scientific papers known to the authors. They were examined and categorized according to model approach used, species and region of implementation. Of these, six case studies each representing a different model type were selected and are presented in the subsequent section for illustration. The review continues with a discussion of the assumptions and limitations of combined models and finishes with a section of pending problems and considerations for future com-

bined models. The reviewed models are listed in the bibliography section that precedes the literature citations.

### **2.3 - Overview of published models worldwide**

The fisheries models that incorporate climatic and/or environmental factors are designated in this review as “combined models”. They are examined with respect to the type of resource modelled (fish, invertebrate etc.), the environmental factors they incorporate and how and if these are connected to the biological parameters of the resource population. The assumption is that both empirical relations and known mechanisms between performance of a stock or that of its fishery and environmental variables are valuable for the use in combined models. Equally both inductive and deductive reasoning is considered possible to achieve valid results; the basic intention here as that of the entire review is to give examples that overcome the idea that models used in the assessment of marine resources need to consider fishery pressure as the sole extrinsic factor important for population dynamics. With only one exception, all of the models reviewed found an important influence of EV/CV on their modelled target and emphasized the importance of the inclusion of such extrinsic factors for valid results and prediction.

Only one of the reviewed models (INP 2000, abalone of the central Baja California peninsula, surplus production model with linear dependency of growth rate to EV) to our knowledge has been used in the management of the assessed species. Some of the publications (e.g. Planque et al. 2003, Shannon et al. 2004) explicitly mention applicability of their models for management purposes. It is difficult to decide whether or not the results of the reviewed models have as yet produced different management decisions. One should assume that the models reviewed should greatly alter and possibly improve management decisions once the environmental influence on the resources is accepted by fisheries managers.

The following model types are distinguished and described: stock-recruit-analysis (SRA), surplus production models (SPM), structured models (SM), general additive models (GAM) and individual based models (IBM). Models that do not belong to these categories were merged within the group “other models” (OM). For each model an example is given, which represents the taxonomic group mostly addressed by the respective model type. Model classification is not always easy; in particular the SRA in the often used form

for the calculation of recruitment success ( $\log(R/S)$ ), may be seen as a special form of the GAM. Especially SM – but other model types as well – often use SRA compartments to compute the first age class.

The marine populations subjected to combined models in the present paper were grouped into four categories: small pelagic fish, all other fish (“pisces”), molluscs and crustaceans. An additional fifth cluster, named “other” is comprised of all other taxonomic and functional entities, such as the functional group plankton or, as in the case with the Ecopath with Ecosim (EwE) models, an ecosystem as a whole. Models of terrestrial populations incorporating CV/EV were not considered here.

Figure V-4 provides a global overview of the distribution of the published climate-fisheries models reviewed; Table V-1 lists the models by model types. Most were designed for resources of the northeast Pacific and the epicontinental seas of the North Atlantic, which reflects the greater advancement of fishery science and greater financial input in the developed countries of the northern hemisphere. The region group “epicontinental seas”, the second biggest group, comprises the Baltic Sea, the North Sea, the Barents Sea and the Black Sea. The four GAM of Daskalov (1999) were constructed for fish stocks of the Black Sea. The far greater number of models of the northeast Pacific region compared to the European side of the Atlantic and its adjacent epicontinental seas may be the result of a more traditionalist way of doing fisheries science in Europe. Other reasons may originate in the general decline of fisheries catches in European waters and with it possibly a decreasing dedication to fisheries science in Europe. The high number of models constructed for the first two taxonomic groups (small pelagics and other fish) reflects the economic importance of these for global fisheries. Nearly all combined fishery-EV models were designed in the last five years. The first combined models known to the authors of the present review were those for cod and yellowtail flounder of the Gulf of Maine by Loucks & Sutcliffe (1978), where SST was included via a Ricker stock-recruitment relationship. The original work of Ricker (1958) on this model was not included in the table as the author developed his work considering a nonexistent, “artificial” fish stock. The traditional SRA and SPM based on the work of Ricker (1954, 1958) and Schaefer (1954, 1957) were the most widely used approaches, followed by the general additive model (GAM). The SRA and SPM models were used mostly in the oceanic realms adjacent to developed countries of the northern hemisphere. The group of models

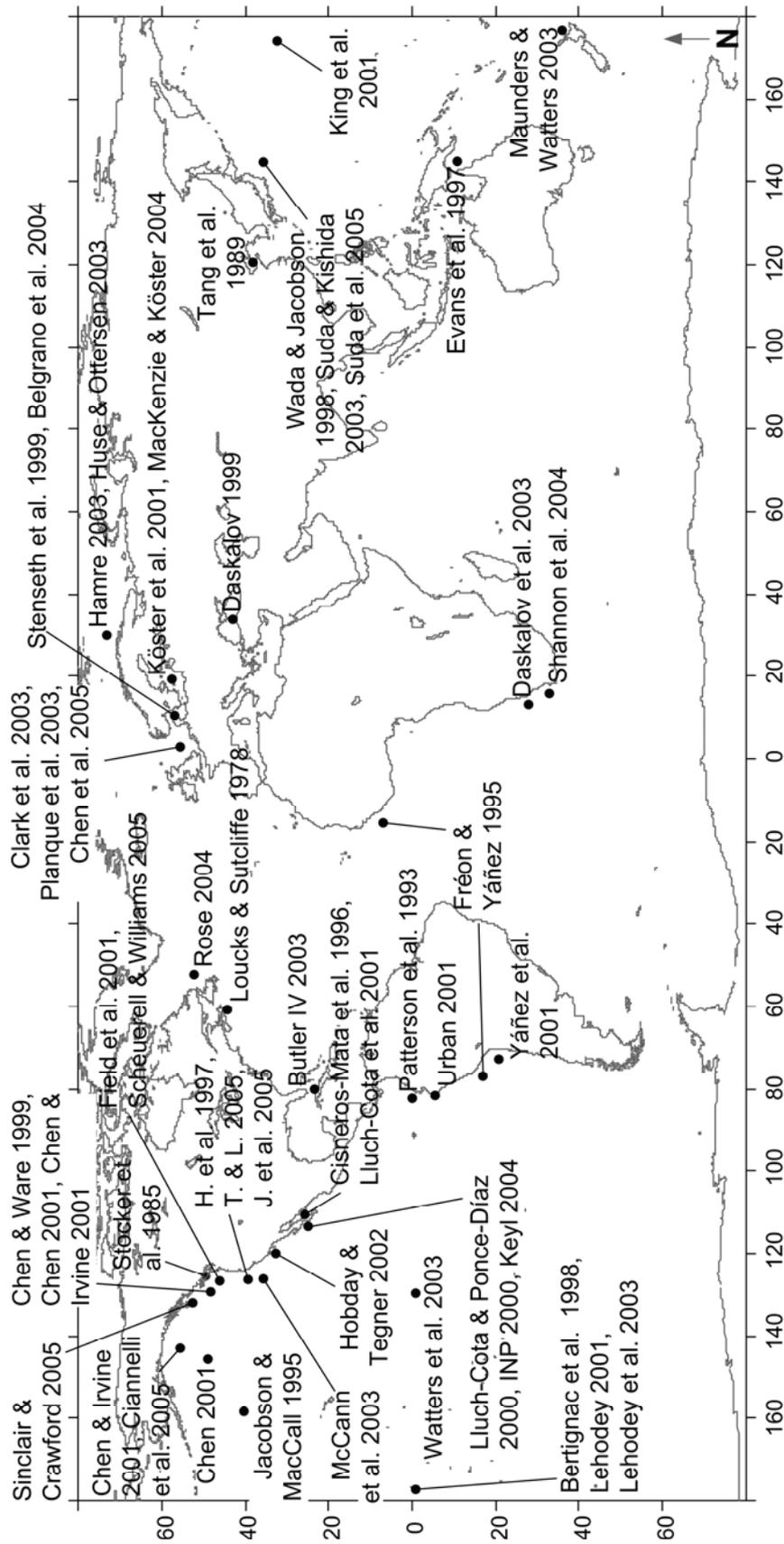


Figure V-4: Combined fisheries-climate models considered in the present review and their global distribution; H. et al. 1997; Higgins et al. 1997; T. and L. 2005; Tolimieri and Levin 2005; J. et al. 2005; Jacobson et al. 2005; not shown: Klyashtorin (2001) various clupeid stocks in Atlantic and Pacific

denominated “other models” consists of a multi-species model (Hamre 2003), artificial neural network models (ANN, Chen & Ware 1999, Huse & Ottersen 2003), a double logistic model to describe probability of spawning (Lluch-Cota et al. 2001a), sinusoidal models (Klyashtorin 1998, 2001), a timeseries model (Scheuerell & Williams 2005) and EwE models (Watters et al. 2003, Shannon et al. 2004).

The relative high number of models in this last group suggests that the traditional model types (SPA and SPM) do not always yield satisfying results and give insufficient flexibility. We expect that the use of the traditional model types will further lose ground to the more complex models.

## **2.4 - Case studies**

In this section we present six published models in more detail. We think that these are somewhat representative for their group and include most of the features, strengths and weaknesses of its model type. For each of these examples, the resources modelled, type and extent of the data required were evaluated, the EV considered and the general hypothesis given. Main results and conclusions were examined, illustrated and discussed. Special attention was given to the inclusion of spatial factors and to the question if and how stock forecast was achieved as well as to the potential temporal forecast distance. Additionally the question was addressed if a comparison of the reviewed “combined” models with a “traditional” version of it without the inclusion of EV/CV was accomplished to decide if the expanded model improved prediction performance. This evaluation was not done in all cases and only few publications used a quantitative method as the Akaike Information Criterion or the Schwartz Bayesian Criterion (see e.g. Kuha 2004) that is able to compare the quality of model approaches with different parameter numbers. As a model fit to a data set usually increases with higher parameter number of the model the use of such a criterion is of utmost importance for the decision if a model amplified by the inclusion of EV (i.e. the addition of parameters) really is the better choice.

Results of the six models studied closer showed an influence of environmental factors on biological processes governing population dynamics in nearly all cases as e.g. temperature or a mix of such factors as represented by climate indices. Nevertheless, a full understanding of the mechanisms behind the observed relationships is rarely possible with the chosen ecological modelling approaches. While these approaches allow for a formulation

**Table V-1: reviewed fishery models incorporating EV by model type and species, Cr: Crustacean, M: Molluscs, SRA: stock-recruitment-analysis, GAM: generalized additive model, IBM: individual-based model**

Species	SRA (14)	Model type				Other Models (11)
		SPM (12)	GAM (9)	Struct. Mod. (9)	IBM (3)	
Small Pelagics (21)						
Anchovy (5)		Fréon and Yáñez 1995, Yáñez et al. 2001	Daskalov 1999			Klyashtorin 1998, 2001
Herring (4)	Stocker et al. 1985, Chen and Ware 1999, Chen 2001, Chen and Irvine 2001					
Sardine (12)		Fréon and Yáñez 1995, Yáñez et al. 2001, Jacobsson et al. 2005	Jacobson and MacCall 1995, Daskalov 1999, Daskalov et al. 2003	Cisneros Mata et al. 1996, Suda and Kishida 2003	Suda et al. 2005	Klyashtorin 1998, 2001, Lluich-Cota et al. 2001
Small Pelagics (21)						
Bocaccio	Tolimieri and Levin 2005					
Cod	Loucks and Sutcliffe, 1978, Planque et al. 2003, Sinclair and Crawford 2005	Rose 2004		Köster et al. 2001, Clark et al. 2003, Chen et al. 2005		Huse and Ottersen 2003
Hauraki Gulf Snapper				Maunder & Walters 2003		
Mackerelspp.			Patterson et al. 1993, Daskalov 1999			
Pacific Halibut	Chen 2001					
Salmonspp.	Chen and Irvine 2001, McCann et al. 2003					
Tuna		Lehodey 2001, Lehodey et al. 2003		Bertignac et al. 1998		Scheuerell and Williams 2005
Walleye Pollock						
Whiting			Ciannelli et al. 2004			
Flounder	Loucks and Sutcliffe, 1978		Daskalov 1999			
Dungeness crab	McCann et al. 2003					
Prawnspp.	Tang et al. 1989					
Spiny lobster		Evans et al. 1997				
Cr. (5)				Higginset al. 1997	Butler IV 2003	
M.(5)		INP 2000, Keyl 2004, Lluich-C and Ponce-D 2000			Hobday and Tegner 2002	
Gari solida					Urban 2001	
Ecosystem						Field et al. 2001, Watters et al. 2003, Shannon et al. 2004a, b
Multi-species						Hamre 2003
Phytoplankton			Belgrano et al. 2004			

of basic hypotheses of underlying mechanisms, a full understanding requires further biological investigation.

For any further details of the models presented here, the interested reader is directed to the original publications.

### **Stock-Recruit Analysis (SRA): Chen & Irvine (2001)**

Chen & Irvine (2001) use an approach based on the logarithmic transformation of the Ricker stock-recruitment model that includes fishery pressure and a set of environmental factors. The novelty of their approach is the inclusion of several factors by the use of a non-linear function describing extrinsic influences of the environment and the impacts of the fishery. By a nonparametric smoothing approach the model is fitted to data and a bootstrap method is used to estimate parameter uncertainty, important for the formulation of management goals. The model was applied to two exploited resources of the northeast Pacific: the pink salmon (*Oncorhynchus gorbuscha*) with SST as environmental variable and the herring (*Clupea harengus*) of the west coast of Vancouver Island (WCVI) where SST and hake biomass (an important herring predator) were included as variables.

The results for the pink salmon population showed that the inclusion of an environmental forcing factor (sea surface temperature) improved the fit of the models to the fisheries data. The Ricker model solved with the classical regression analysis was only statistically significant when SST was included as environmental variable. In the next step the non-parametric solution of this model was tried, which improved the fit. In the case of the WCVI herring population spawning stock biomass (SSB), SST and hake biomass—as a biotic environmental factor—were included in the model of this resource. The simple S–R model that did not include any type of EV was already significant, but the fit greatly increased with model complexity and the inclusion of EV. Thus the semiparametric model that includes EV non-linearly clearly explained recruitment data of both stocks better than the simpler models of Ricker (1958) and the extended log-transformed model. A SST time series as employed in the above models is often used as an environmental factor as its influence on individuals and populations is well described. An attempt to forecast future stock size or recruitment numbers by using the created model and a forecasted SST series was not attempted by the authors nor was the further validation of the result by the

application of an information criterion as that of Akaike to eliminate the possibility of a better fit due to higher parameter number.

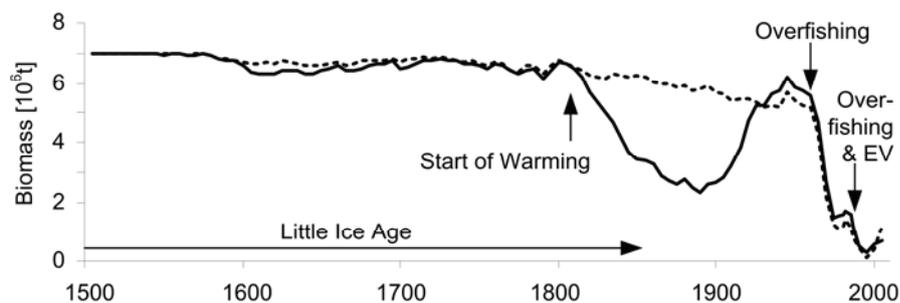
Generally data requirements for the SRA are moderate but the required knowledge of recruit numbers may prevent its application in fisheries with scarce to no survey data or limited age-or length-structured data. In the present study the nonlinearity of the relationship between biological or ecological and environmental variables is confirmed and solved through the use of a nonparametric fitting method. Clear relationships between SSB and recruit number have been doubtful for fish and invertebrate populations (e.g. Koslow 1992, Iles & Beverton 1998) but nevertheless the SRA-approach has been often used and also has been included in structured models of marine resources (see below).

#### **Surplus production models (SPM): Rose (2004)**

The model of Rose (2004) examines the effects of fishing pressure and climate variability on the cod (*Gadus morhua*) stocks of Newfoundland. Data used were fisheries landings and environmental data from 1505 to 2004 reconstructed from published historical landings and tree ring series. Cod biomass was calculated by means of a SPM based on estimates of the catch per unit of effort (CPUE) derived from the human population size of Newfoundland and Labrador which was assumed to be directly linear to fishery effort. The author compared several models with and without fishing pressure and climate effects via the model's parameters of the population's intrinsic growth rate. The environmental variable used was a long time temperature series retrieved from growth chronologies of white spruce and cedar of the northern North American continent and from instrumental time series of Greenland that were strongly correlated in the overlapping period. EV was included into the model linearly.

The main result of this approach was that constant values for intrinsic growth rate cannot explain the historical (little used stock) and recent (heavily exploited stock) data at the same time. Only the combined climate variability-fishery model was able to explain the decline in the mid to late nineteenth century, the collapse of the 1960s, the collapse of the 1980s and the missing recovery of the stocks in the last decades. It is assumed that these phenomena were caused by the warming after the Little Ice Age (LIA), overfishing, the combined influences of CV and fishing and the depensatory effects of the small stock size respectively, as shown by the arrows in Figure V-5.

The author wrongly assumed the LIA to have lasted from 1800 to 1880, while it is usually assumed to have lasted from the fifteenth to the nineteenth century (Houghton et al. 2001, Esper et al. 2002, Oerlemans 2005). The period mentioned by Rose (2004) must actually be interpreted as the relative rapid warming or “regime shift” that led into the present warm phase. The combined model was not connected to large-scale climate indices that would have made it possible to predict future yields of cod in the area and to utilize the model in stock assessment and management. Only one of the other examples of combined SPM (Keyl 2004) did use climate indices that may enable these models to forecast future fishery yields.



**Figure V-5: Results of the SPM model designed for Newfoundland and Labrador cod; dashed line: classic SPM without inclusion of EV; black line: final combined SPM incorporating EV and depletion in  $r$  and  $K$  (modified after Rose 2004)**

General advantages of the SPM are their possibility to be implemented as simple spreadsheet models and to use official records of landings and effort data of every fishery. This enables the implementation of this model type for populations and stocks, for which further survey data are scarce or non-existent (Quinn & Deriso 1999, Haddon 2001). In the present example it was possible to use the SPM even with the meager historical data. Data scarcity, particularly in developing countries or for new fisheries, is often a valid reason to choose SPM. The main characteristic of SPM is the (over) simplified description of population dynamics in the form of just two model parameters: the intrinsic growth rate ( $r$ ) expressing all density-independent factors of the population and the carrying capacity ( $K$ ) expressing all density-dependent ones. Effects of exogenous and endogenous factors cannot be distinguished nor can they be allocated to single functions and pathways that govern the fluctuations of the modelled population (Megrey & Weststad 1989). It might therefore be difficult to relate EV to biological variables like mortality or fecundity controlling population dynamics. However, Stenseth et al. (2003) consider this

even as an advantage under certain circumstances (see below). Fréon & Yáñez (1995) published an expert system called CLIMPROD that can be obtained from FAO and allows building SPM with up to two exogenous factors but to our knowledge only two additional publications have as yet used CLIMPROD (Evans et al. 1997, Yáñez et al. 2001).

### **Structured models (SM): Higgins et al. (1997)**

The eight models presented in Higgins et al. (1997) estimate the intensively exploited populations of the Dungeness crab (*Cancer magister*) along the northeastern Pacific Rim. The basis for the combined models is a deterministic, non-spatial model with an egg state and four age class compartments that differ between male and female compartments. The number of eggs is determined via a Ricker-like equation that includes a basic density-independent and a density dependent part of fecundity. Only four-year-old and older males are harvested and it is assumed that the highly variable catch directly reflects the population dynamics. The authors assumed that environmental forcing on all age classes is similar. Total environmental perturbations were estimated by comparing the observed with the predicted catch by the deterministic model, i.e. the model residuals are assumed to be due to environmental factors only. The environmental perturbation was included exponentially in age classes one to three without relating it to observed series of any specific environmental variable.

Results show that the model predicted the observed catch data of the next year very well. The error (environmental perturbations) was much smaller than the amplitudes of the catch fluctuations and all eight basic deterministic models produced stable equilibriums of catch. For the inclusion of EV in the basic deterministic models highly variable time series were created by deriving the stochasticity from the errors of the deterministic model. The resulting fluctuating catch series over 1,000 years of the final combined models were consistent in its mean and variance with the observed data of the second half of the twentieth century. The authors concluded that environmental perturbation that by the authors is considered of stochastic nature is responsible for the catch variability observed. They stated that the dynamics of the Dungeness crab is a product of combined endogenous (density dependent) and exogenous (fishery and EV) factors. Their results suggest that even when EV (represented by the residuals of the deterministic model) is low it produces great fluctuations and has therefore to be included into assessment models. Due to the stochastic inclusion of EV a “real” forecast is not possible with this model.

We consider the work of Higgins et al. (1997) as a very important contribution to the understanding of combined modelling as it shows the general importance of the incorporation of EV in population models even if considered stochastic. The conclusions drawn are that 1) an inclusion of fishery pressure as sole extrinsic factor is not sufficient as 2) relatively small residuals are responsible for the high variability of model results. 3) The observed residuals are not due to process errors or artifacts in the models but to environmental variability, and 4) relations between EV and the growth of the population are non-linear. Requirements for this model approach are limited to fishery data and a general knowledge of the life history of the population. However, for use in assessment and catch forecasting the models would need to be related to ‘‘real’’ environmental data, i.e. to relate the errors of the deterministic model to CV/ EV timeseries. A further difficulty may be the novel and advanced method of data fitting described as a mixture of three different sophisticated methods.

#### **Trophic multispecies models: Watters et al. (2003)**

A trophic model with 38 functional compartments built with the program Ecopath with Ecosim (EwE; Walters et al. 1997) by Olson and Watters (2003) served to evaluate the influences of physical effects on the eastern tropical Pacific (ETP) ecosystem. The authors assume that this ecosystem is affected by the ENSO via changes in primary production and predator biomass and therefore inflicted physical forcing of these compartments. In a first scenario, just the phytoplankton compartment was exposed to environmental forcing, while in a second the recruitment of predators and vulnerability of their prey was added. The objective was to simulate both indirect and direct effects of ENSO on the middle and upper trophic levels of the ecosystem. In both scenarios the ecosystem model was forced by a suite of different environmental factor trajectories to further clarify the influence of EV: trajectories with cold and warm single pulses, others with cycles of two to six year duration and different temporal distances between cold and warm pulses, a trajectory of the Niño3 SST-anomaly series from 1900 up to 1999 and that of the predicted SST-anomalies of different coupled ocean/ climate models (GCM). The environmental factor trajectories were related exponentially to biomass, recruitment and vulnerability. One simulation was done without fishing pressure; all others included fishing mortality based on a calculated average of previous years.

The model runs of the “bottom-up” scenario that used the “large plankton” biomass forcing series as a result for all trajectories yielded a lagged and propagating oscillation after a perturbation simulated by single positive and negative pulses or oscillations. The trophic level of the ecosystem compartments positively correlated to the lag and negatively to the amplitude of the response oscillation. Negative perturbations had higher impacts but no component of the system became extinct or showed other significant stable changes. After some time the system always returned to its initial state. In the second, the complete scenario that simulated a combined “bottom-up/top-down” environmental forcing the higher level compartments did not show the same lag as before but immediately oscillated to the opposite direction of the “large phytoplankton” compartment. This behaviour was due to the recruitment trajectory of the predator compartments and the vulnerability trajectory for their prey. After the first oscillation following the perturbation the higher level biomass trajectories of this scenario fell into phase with the trajectories of the same compartments of the first scenario. The forcing trajectories retrieved from the Niño3 SST-anomaly series in the second scenario showed a great increase in general biomass variability of the higher trophic level compartments. Negative correlations between high trophic levels and “large phytoplankton” were higher than in the first scenario. Global warming trajectories predicted by the GCM showed that components with low total mortality ( $Z < 0.5$ ) were not very sensitive to ENSO-scale forcing during global warming but, in general, global warming had an important impact on the system. The authors stated that under constant fishing pressure physical factors dominate the regulation of the inter-annual fluctuations of the consumer compartments of the modelled ecosystem. General conclusions drawn are that single-species models are not suitable for the detection and interpretation of the (lag) response of different system compartments to EV or CV. Scenario 2 with bottom-up/top-down forcing appears to be more realistic as it is also supported by results of previous work by Micheli (1999). Direct forcing on middle and upper trophic levels can be the dominant source of variability of populations and ecosystems. Watters et al. (2003) explained the higher recruitment of the upper trophic levels during negative anomalies of the “large plankton” by assumed constant picoplankton levels (thus little affected by EV) in the EwE-model. In our opinion this might only be an artifact of the constructed model as this compartment was not directly forced by the environmental factors. The authors further stated that the downward cascading effect of fishing is less if EV is directly influencing the higher trophic levels (scenario 2). Through interspecific and intra-specific effects, many biomass trajectories behaved in a complex

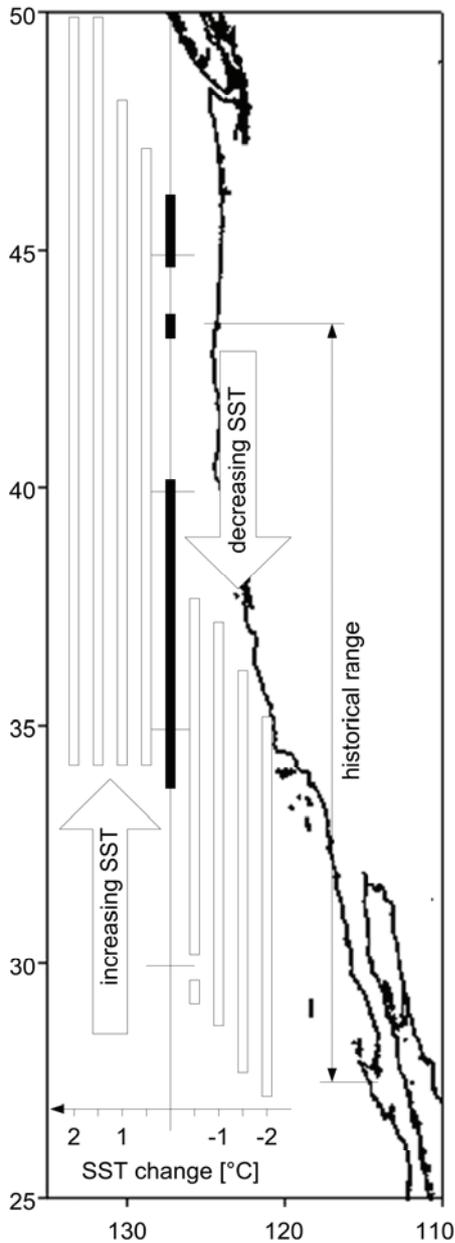
manner and showed similarities to superimposed waves in spite of the simple original forcing functions. Influences of climate and environmental variability were included via the ENSO-related Niño3-series that is predictable up to around six to nine month (see forecasts on the CPC web page). Decadal-scale oscillations like the PDO were not investigated in this trophic ecosystem model.

A general problem of the EwE-models is that they are extremely data demanding and based on a “snapshot” of the “balanced” system. Thus “average flow conditions” are assumed for the baseline model, while the system may well be going through a great dynamic change at the same time. Possible spatial effects of EV and CV are to our understanding as yet difficult to handle with this model. A great advantage of this approach is that impacts of the environment and of the fishery on the ecosystem as a whole and on each of its functional groups can be explored simultaneously. Ecosystem based management practices can thus be evaluated with regard to their negative and positive effects on all relevant biotic compartments within the system.

#### **Individual based models (IBM): Hobday & Tegner (2002)**

The aim of this individual-based approach was to investigate the extinction risk of two red abalone (*Haliotis rufescens*) populations in the Southern California Bight, USA under different environmental scenarios and to predict the latitudinal extension limits along the Pacific coast of North America. The central hypothesis was that red abalone are sensitive to water temperature changes in their habitat and that future warming might strongly influence their survival in their present settling locations (cold and warm) in southern California. The spatial explicitness of the simulation allowed the investigation of potential effects of a reserve area protected from fishing. Model parameters and individual life history values were taken from previous work on abalone; the model distinguished between larval, juvenile and adult stages, each with specific characteristics respective to survival and the effects of the influence of SST. EV and biological performance were linearly connected.

The results supported the initial hypothesis that the survival of red abalone populations in California is highly sensitive to temperature changes. Extinction was forecasted by all model runs for mean SST-values below 11°C and above 16°C, suggesting that the popu-



*Figure V-6: Calculated latitudinal distribution ranges of red abalone off the Californian coast in relation to SST changes; 0 is the present mean value at every geographical location (black bars indicate calculated distribution at present temperatures (modified after Hobday and Tegner 2002))*

lation of the warmer habitat is in danger of becoming extinct with any further warming. Applying fishing pressure strongly decreased population sizes in co-dependency of SST in all scenarios and increased the risk of extinction. The highest possible fishery landings were found for SST between 12°C and 13°C, and fishing pressure under “bad” (warmer water) conditions had a much higher effect than under conditions of “good” SST. The addition of a no fishing reserve had beneficial effects on the population: time to extinction was greatly increased and the overall stock decrease due to fishing was lowered.

Very important is the result that the distribution limits of abalone varied strongly with varying SST (Figure V-6). With increasing temperature the southern limit moved further north and the traditional red abalone fishing areas were not suitable for exploitation any more or the populations even became extinct if not protected from fishing. We assume that, generally, by using combined models, observed migratory patterns can be explained and predicted as is shown here for abalone distribution of the North American Pacific coast. The findings of Hobday & Tegner (2002) indicate that for the sustainable management of abalone stocks the creation of reserves will be necessary. For their successful implementation (and site selection) a forecasting of future EV may be crucial. The IBM built in the present example were not connected to observed decadal or even larger scale oscillation indices, but the authors used constructed SST time series that more or less simulated the regimes observed.

The individual-based approach can include virtually every parameter and function of a target population and can also be used to design multi-species models. Still more important is the fact that IBM can easily include spatial factors that are often of importance for the dynamics of populations (see examples in Grimm & Railsback 2005). Models of this type cannot to be transferred to other populations, either of the same species in other locations, nor for other species, as they very explicitly describe the situation of the population for which they were originally designed. The individual-based approach is the only form to address the effects of individual variability within a population. Temporal requirements to learn the method and to construct the models are high, but results seem to often justify these efforts (Grimm & Railsback 2005).

### **General additive models (GAM): Daskalov (1999)**

GAM differ from the other model types as they do not explicitly refer to intrinsic functional factors regulating the fluctuation of populations. Instead, they build on empirical relations between data series. Nevertheless they were included in present work, as they may often be a first if not the only possibility that does not rely on linear relationships between biological performance and EV/CV (see next section below) to assess an exploited stock and help to understand underlying mechanisms by induction.

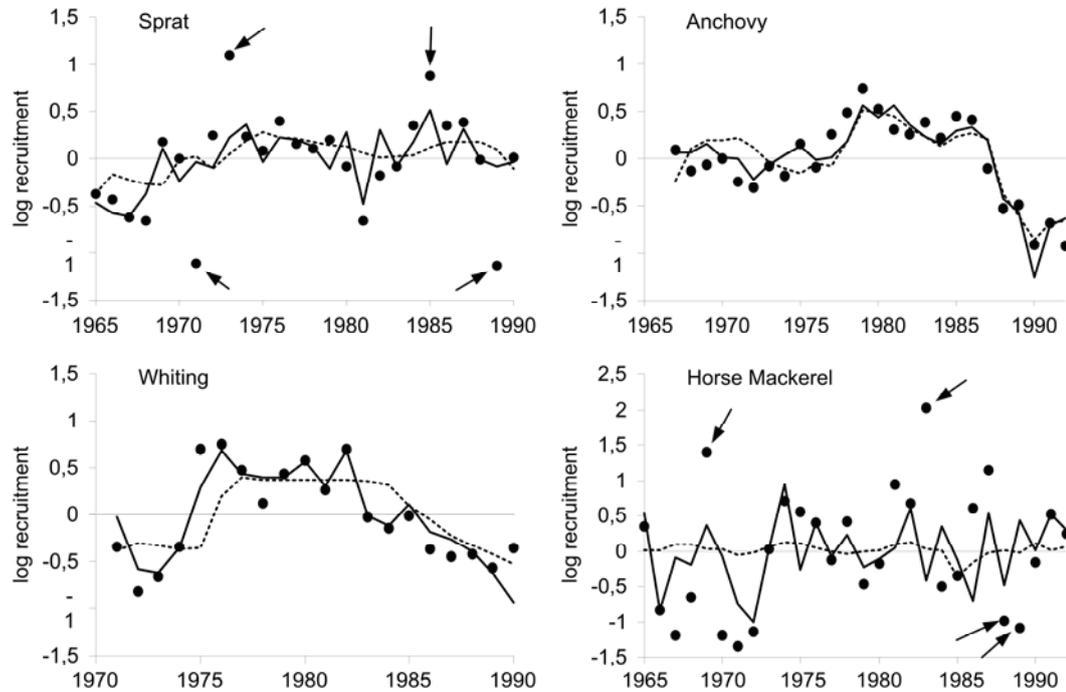
The goal of Daskalov (1999) was to relate the size of the parental stock and several environmental factors to the recruitment strength of four Black Sea species of commercial

interest (sprat, anchovy, whiting and horse mackerel) by means of four separate GAM. Additionally, the author wanted to demonstrate the general suitability of GAM for marine stock assessment when the dynamics of populations depend on a mixture of biotic and abiotic factors. In the example given, the author tests for a relation between recruitment success spawning stock biomass (SSB) and the following abiotic factors: SST, wind speed, wind stress, wind mixing, sea level atmospheric pressure (SLP) and river run-off. As the GAM of Daskalov relate SSB to recruitment they can be interpreted as a non-linear SRA.

The results support the basic hypothesis of Ricker (1958) according to which, both SSB and environmental factors are important for recruitment. Models with the best fit to data for each species incorporated two abiotic factors in addition to the SSB; in two cases a constructed principle component series representing the variability of all abiotic variables were included. Contrary to the widely accepted importance of SST, this factor was only included in the model for horse mackerel. Figure V-7 shows that the different environmental variables markedly improved the models' performance. The data points marked by arrows cannot be explained by the models, yet we assume that these extreme year classes might be very important for the fishery. They might also hint to the problem that GAM do not explicitly describe the mechanisms that control fluctuations in the populations but just describe empirical relationships between data series. The results suggest that the mechanisms controlling recruitment are complex and may directly as well as indirectly act through a hardly detectable causal chain. Daskalov (1999) suggested that dome-shaped (see Figure V-3) and U-shaped functions of the biological response to environmental factors are common. This is consistent with ecological theory (law of tolerance of Shelford, see e.g. textbooks of Margalef 1998; Townsend et al. 2003) and with other models reviewed here (Lluch-Cota et al. 2001a, Daskalov et al. 2003, Keyl 2004).

The non-linearity found might also explain part of the often observed "breaking relations" between biological and environmental factors described by Myers (1998) and Walters and Korman (1999, and see below). Predictions of the future development of the Black Sea fish populations were not attempted, nor were the environmental series forecasted or related to larger-scale climate variability. The PCA loading series created by the author are, however, similar to other regional indices (MEI or PDOI, see Wolter & Timlin 1998, Mantua et al. 1997 for further details) and might show predictable cyclicity that

eventually can be used for the forecast of the population fluctuations modelled by the GAM.



**Figure V-7: Results for the GAM; circles: observed values; dashed line: GAM including the particular spawning stock biomass (SSB); black line: GAM including SSB and relevant EV; arrows mark: observed data points that can not be explained by the models (modified after Daskalov 1999)**

GAMs are straightforward and easy to understand. Use of the method of nonparametric fitting of the different functions is not widespread, but standard statistical packages include tools to solve it. The great advantage of this modelling approach is that all types of function can be applied to connect the predictors to the (biological) response variable, without the need to specify the relationship beforehand. Spatial considerations were not made and would be somewhat difficult to include in a GAM. As already mentioned, the missing theoretical basis of the biological functions and factors governing the population dynamics may be a deficit and may greatly complicate the interpretation of the results. However, GAM are important exploratory tools to empirically detect basic interrelations and surely can be used successfully in resource assessment and management.

## **2.5 - Problems pending and considerations for future combined models**

### **“Breaking relationships” between environmental factors and the biological performance**

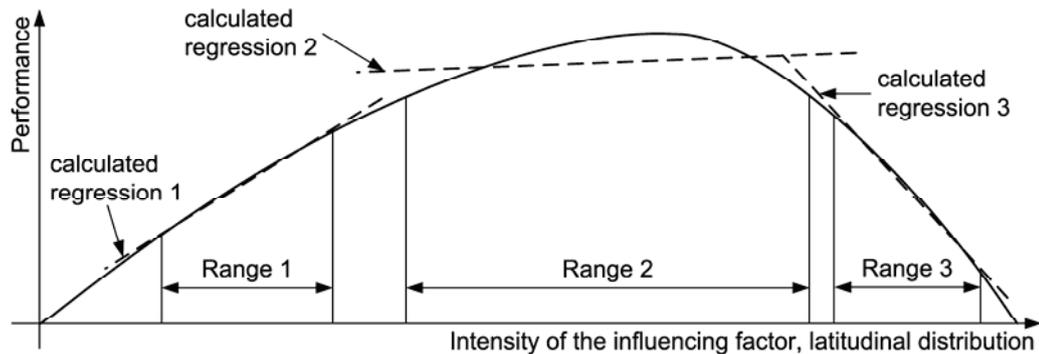
One of the basic challenges but also the primary goal of combined models is to understand the “real” mechanisms behind empirically determined relationships between EV/CV and the compartments and interactions of an ecosystem. It has often been reported that relationships that were found by the analysis of time series broke down as soon as they were published (Daniel Pauly, personal communication and see the review by Myers 1998) or changed in different periods (Skud 1982; Solow 2002). We offer the following seven possible reasons for such “breaking relationships” that may help to prevent these. To our knowledge these arguments have not yet been considered before to respond to the general problem shown by Myers (1998).

#### **NON-LINEARITY**

As is shown by biochemical (e.g. the Q10-rule) and ecological theory (Margalef 1998, Townsend et al. 2003) organismic response to the intensity of an extrinsic factor is rarely or never (Steele 2004) linear. The problem is that most common statistical methods used (e.g. regression, ANOVA) are of a linear nature and are used as basic tools in natural and social sciences. To parameterize and solve for non-linear relationships most of these methods must be modified or at least extended or new methods must be developed. Although non-linear tools are now included in most statistical software packages, most of us are still not as familiar with those as with the traditionally used linear methods. Some of the models reviewed here (the GAM, Daskalov 1999, Daskalov et al. 2003, Belgrano et al. 2004, Chen et al. 2005) were based on methods found in these statistical packages, while other researchers used novel approaches (Higgins et al. 1997, Chen & Irvine 2001) to include non-linear relationships into their model designs.

The hypothetical example given in Figure V-8 clarifies this idea. It shows a skewed double-logistic function that describes a relationship between an environmental factor and a biological response. By wrongly assuming a linear relationship between the two (e.g. due to a restricted range of available data) the resulting linear correlation will necessarily produce misleading conclusions regarding the influence of an environmental factor (over its

total range) on biological performance. In our opinion, this has been a common situation in many studies, since available data series may have only covered parts of the relevant range of values of an environmental factor. The problem of the use of linear methods on non-linear relationships has been addressed before e.g. by Gargett (1997) and Baumann (1998).

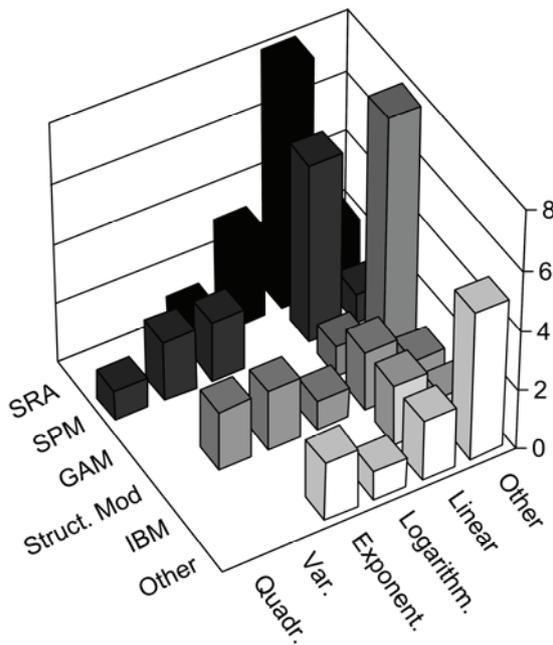


*Figure V-8: Schematic illustration of “breaking relationships” due to the range of observed values of an influencing factor in three different climatic regimes or for populations with different spatial distributions.*

The models reviewed here use different functions to describe the dependency of the biological response to environmental factors (Figure V-9). Linear functions were most often used followed by the group of models using exponential and logarithmic functions. The group “other” is mainly comprised of the functions found by the GAM that many times were not explicitly specified but were often similar to polynomial relations of different orders. All in all, nearly half of the models used linear functions to describe the relationship between EV and biological performance. Four models incorporated EV and CV by more than one type of relationship, i.e. one biological variable may have been connected to EV via a quadratic function, while another may have been considered linearly.

#### MULTI-DIMENSIONALITY

It is hardly imaginable that only one environmental factor is relevant for the performance of a biotic entity (e.g. Solomon 1949, Fry 1971, Baumann 1998, Rose 2000, Stenseth et al. 2003). Limiting conditions caused by an unobserved factor may thus prevent an observed variable to behave the expected way. Fry (1971) classified these types of variables as “masking factors” that not only act as limiting factors as described by von Liebig (1855) but also may change the basic function of another factor itself. Exemplary cases



*Figure V-9: Mathematical functions used with the different model types; var: various different functions used*

are the iron-limit situation in the Southern Ocean that inhibits higher primary production in spite of the high nitrate and phosphate concentrations in the water that may define phytoplankton communities (Falkowski et al. 1998, Smetacek 1998) or the higher susceptibility of organisms to environmental disturbance after accumulating toxic heavy metals often described. The “optimal window” concept of Cury & Roy (1989) describes the multifactor problem and shows for clupeid fish in upwelling systems, that recruitment is greatly a function of the two factors; upwelling intensity and turbulence. More than two decades ago Skud (1982) investigating the interactions of small pelagic species pairs and EV/CV influence suggested to never consider the influence of climatic factors without taking into account abundance structures between species, i. e. to consider the mixed biotic/abiotic multi-dimensionality of the extrinsic influences on the performance of a species. Oscillatory bifurcation of model results due to multi-dimensional forcing of ecosystems and its compartments is observed already with quiet simple models and is another possibility that leads to breaking relationships resulting from different pathways when reaching high values of the environmental factors from rather low ones and vice versa (e.g. Steele 2004).

#### DIRECT AND INDIRECT IMPACTS

It can be assumed that many factors do not only have direct effects on the ecosystem but also indirect ones via complex chains of interactions that may further mask, mitigate or

intensify specific functions. Water temperature is used as an example here. As most marine organisms are thermal conformers and even small changes in the surrounding temperature will influence individual metabolism (Jobling 1996), it is widely established that varying SST correlates with changes of primary production, individual growth, fecundity, spawning time, movement, distribution and migration patterns, to mention just a few. It is thus important to take the possible existence of an interaction between direct and indirect effects of the changing environmental variables into account.

#### TEMPORAL LAGS

Further concealing of the effects of environmental factors may also be based on temporal patterns and a lag response of the biota (McCann et al. 2003). Due to the simple fact that life spans of organisms are often longer than relevant influencing oscillations, the impact of changing environmental conditions on ecosystems may not be immediately noticeable. The traditional SRA consider this phenomenon: recruits depend on the number of eggs and larvae that in turn depend on the spawning stock size. Fishing on the adult stock thus has a delayed influence on the number of future recruits that also depends on the size of the “survival window” from egg to recruit. The latter is largely controlled by abiotic factors (Wolff et al. 2007 and examples in Stenseth et al. 2003).

#### SPATIAL CONSIDERATIONS

The incorporation of EV/CV produces the necessity for modelers to consider space and related phenomena like distribution or migration more profoundly than with “classic” models that do not incorporate EV/CV. This is important as many of the relevant environmental variables not only vary temporally but also along spatial gradients, e.g. due to latitudinal or vertical effects. Local characteristics based on the morphology of every geographical point on earth will also produce changing conditions of the factors important for the performance of an ecosystem. The question to be asked is: “what are the [...] changes in the distribution and abundance of species relative to the predicted [...] habitat change in this location?” (Thrush et al. 2005). In the review by Myers (1998), considerations on spatial effects of environmental conditions were not made but might be another reason for the observed “breaking relationships”. The author found rather strong EV/CV-population performance relationships in the limits of a species distribution and rather weak ones in the distribution-center. Planque & Frédou (1999) confirmed this for nine stocks of cod in the North Atlantic where only the stocks found at the distribution

limits showed clear correlation between recruitment success and SST. This is shown on Fig. 6 if one understands that the intensity of a factor (the x-axis) due to the spatial gradient corresponds to the latitudinal distribution area of a species or population. Considering only stocks or subpopulations of parts of the whole distribution area, investigations by (wrong) linear methods will lead to clear positive and negative correlations between biotic performance and environmental factors in the distributional limits. In the distribution centre no or only weak correlation can be found. The importance of spatial considerations was also emphasized by Wolff & Vargas (1994) who showed that the impact of the ENSO warming on several Peruvian invertebrate resources greatly differed with latitude and coastal topography.

Of the 58 models reviewed here only 10 consider spatial effects. Interestingly, all three IBM do so although none of the authors explicitly expressed the importance to consider temporal and spatial gradients of environmental factors at the same time. The model of Hobday & Tegner (2002) calculated the northern and southern distribution limits of abalone of the Californian current system in dependency of the local SST. We assume that changing distribution areas and migratory patterns as response to environmental variability can be explained with spatially explicit combined models.

#### EFFECTS OF POPULATION STRUCTURE

Different answers to changing environmental conditions of different age-classes and following changing links strengths between environment and climate in case of changing age structure of a population (Ottersen et al. 2006) may further explain why described correlations break down when newly reviewed. One of the most common observed results of the exploitation of marine resources is the change in age-structure of the stock. Reviews as that of Myers (1998) that are reconsidering relationships of fished stocks more than two decades ago may therefore yield results different from those of the original publications, as the age structure in the interim are likely to have undergone important changes.

#### SPURIOUS REGRESSIONS

The last possibility for “breaking relationships” given here is of a mathematical nature. Wrong correlations may be produced in cases where the real and the chosen relationships are both similarly linear but uncorrelated. In particular, small auto-correlated series and

using the popular least-square techniques for parameterization the proportion of “spurious” regressions might reach up to 76% of occasions (Granger et al. 2001). All of the preconditions mentioned by these authors are frequently found with natural timeseries of biotic or abiotic sources and should therefore be considered as a possible explanation for the problem of “breaking relationships” between environmental factors and biological performance.

### **“Simplicity vs. complexity” and the search for environmental proxies**

Due to the complexity resulting from multi-dimensionality and direct and indirect effects of EV, the response of most resources and ecosystems to their varying environment are known only to a small extent. It is therefore not trivial to select the proper exogenous variables that are most important for the performance of target populations. Mortality will certainly be controlled by other environmental factors than fecundity or individual growth, and factors that have a positive impact on one type of biological performance might be highly negative for another. It is very likeable that one process (e.g. dispersal of larvae) may be influenced by a specific temporally punctual event like a severe storm while another (e.g. spawning) depends on a constant or mean of a certain environmental factor such as temperature. The different life history stages are again influenced differently by EV/CV and so are intra- and interspecific relationships of a population. Therefore, a thorough knowledge of the life cycles of the populations is required to correctly connect them to their abiotic environment and its variability (Anderson & Rodhouse 2001). However, as long as exact mechanisms of the relationships between EV/CV and systems are not known, the complex biological response to EV may be more successfully related to global climate indices than to any single local climate variable (Stenseth et al. 2003). Klyashtorin (2001) even found a higher correlation between global climate indices and global fishery production as that between local variables and fishery production.

Multivariate indices were developed to represent complex oceanographic and atmospheric variability in time and space and it seems advantageous to relate these large-scale climate indices to the overall performance of biological entities in order keep things as simple as possible, as long as exact and more specific relations (and the mechanisms behind them) are not exactly known. These indices are assumed to be of quite a regular and cyclic nature (Mantua et al. 1997, Lluch-Cota et al. 2003, Stenseth et al. 2003) and may therefore additionally allow for better and longer term predictions than local environ-

mental variables, which may lack this clear cyclic behaviour due to their complex interaction with local morphology. Only if the impact of an extrinsic factor on populations or ecosystems or their functionality is well known, is the use of time series directly representing the factor advisable.

### **Cyclic oscillations, regime shifts and combined models**

Various attempts have been made to include environmental stochasticity into models and results often showed fluctuations of the target populations of a magnitude and duration as observed (Ricker 1958, Higgins et al. 1997). However, to build models of marine populations that incorporate EV/CV and are also able to make predictions of future stock fluctuations, the future development of the variables representing EV/CV must be known. The inclusion of “real” environmental data in combined models instead of random stochasticity seems now possible and reasonable as local EV originates in the interplay of large-scale EV and CV. The resulting ecosystem variability may therefore be directly linked (at least in certain cases) to indices of CV in combined models (Urban 2001, Lehody et al. 2003, Belgrano et al. 2004, Keyl 2004, MacKenzie & Köster 2004, Chen et al. 2005). Clear advantages in the forecast have populations and ecosystems that can be connected to globally important indices of climatic and oceanographic features (Klyashtorin 2001).

A growing body of work on climate oscillations and regimes suggests that at least large-scale CV is predictable to some extent. While forecasting of the globally important oscillations for resource modelling as proposed by Klyashtorin (1998, 2001) and Keyl (2004) through a simple analysis of past cycles is purely empirical this approach seems sufficient for rough predictions of the general trajectories 30–60 years ahead (Klyashtorin 2001) if the oscillations observed for the last millennia do not change. Another form of models to predict future states of the climate and environmental variables (especially SST) are the physics-based “realistic” general circulation models (GCM) constructed in various institutes of the world with different aims (see e.g. Latif et al. 2001, Palmer et al. 2004).

An example for the use of a large-scale climate index – in that case the Pacific decadal oscillation (PDO) index – is the work of Keyl (2004). The author modelled the dynamics of two exploited abalone species in Mexico by means of a SPM and found population sizes to better relate to the PDO than to local environmental variables like SST, SLH and

upwelling strength. Apparently the “package of weather” (Stenseth et al. 2003) described by the PDO-index represented the “parameter package” of the highly unspecific SPM very well. An example of a “detailed” connection of EV and population dynamics is given in a model of Wolff et al. (2007) for the Peruvian bay scallop *Argopecten purpuratus*. The authors relate the local mean SST during the spawning and recruitment period to the development time and survival rate of the larval stage and relate this to the fishery catches following the recruitment period. As a second predictor variable for the expected catches they used spawning stock size as derived from catches during the spawning period. Usually the main problems when local environmental variables are used in combined models, is that these local variables have to be predicted into the future to be of use in resource assessment. This problem does not arise in the above example of the short lived scallop species: data on annual spawning stock size and temperature dependent recruitment strength can be obtained for every year to predict the annual catch of the next year. Nevertheless predictions that reach further ahead must also be a problem. Clark et al. (2003) coupled a spatially structured model of the population dynamics of North Sea cod to the SST-predictions of the Hadley GCM and predicted the dynamics of the population until 2050. We assume that this kind of combined modelling will increase in importance in the following years as the GCM become more and more detailed.

## **2.6 - Concluding remarks**

We expect that combined models will gain further importance not only in the academic circles of fishery scientists but also as everyday tools used in assessment and management of natural resources. The ever improving capacity to detect large-scale cyclic climatic oscillations allows to realistically consider EV/CV and their effects on population dynamics. Due to the new possibilities given by the now readily available computer power and the latest findings by climatic and oceanographic research, we believe that the next generation of fisheries scientists *sensu* Hilborn and Mangel (1997) has already begun. The increasing awareness and understanding of the importance of nonlinearity, multidimensionality and direct/indirect influences of EV/CV with possible temporal lags will increase the capacity of fishery scientists not to be deluded by apparently obvious relations between abiotic and biotic data, which, as often observed, break down afterwards and lead to wrong conclusions. The paths opened by combined models not only connect biological performance to environmental and climatic conditions but also advance our knowledge on the physiology and ecology of populations and communities. The explicit

consideration of space that has to be considered more carefully in combined models will help to further understand the effects of EV/CV on distribution limits and migratory patterns observed by scientist world-wide. However, the “business” of combined modelling is complex and the selection of relevant environmental factors is always difficult.

Human-induced global change that has become more and more visible in the last decade clearly plays a major role for the observed EV/CV oscillations and patterns and subsequently for the results by combined fishery-climate models. May it be that now, after detecting cyclic oscillation so helpful for combined modelling of natural resources these are already being significantly altered by global change?

**Acknowledgements.** This study was financed and conducted in the frame of the EU-project CENSOR (Climate variability and El Nino Southern Oscillation: Impacts for natural resources and management, contract 511071) and is CENSOR publication 0097.

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## CHAPTER VI: Conclusions

Like most other cephalopods jumbo squid (*Dosidicus gigas*) is a relatively short-lived species with a highly opportunistic life strategy that can and must adjust to variable conditions of its environments to survive as an individual and as a population. The results of the studies of the last three years presented in this thesis have lead to a number of conclusions that highlight the impressive possibilities of this species on the physiological to the evolutionary level to meet the requirements of its changing ecosystems of the Eastern Pacific Ocean (EPO).

As in the rest of the EPO, conditions in the Humboldt Current system (HCS), the study area, are highly variable and although the HCS does not comprise an especially high primary production, the productivity of higher levels exceeds all other marine areas (Chavez et al. 2008). Its productivity is closely related to different water masses and generally the cooler water masses are more productive than their warmer counterparts (Calienes & Guillén 1981, Bertrand et al. 2004, Swartzman et al. 2008). Distribution and extension of the different water masses is related to currents, winds and upwelling phenomena (Morón 2000, Graco et al. 2007, Keyl et al. 2008) and therefore have a strong temporal and a spatial component. Both components must be considered when trying to understand the connections between the physical environment and the entities of the ecosystems.

Oceanographic and atmospheric conditions of the HCS are governed by larger-scale climate conditions and occur in seasonal to decadal periods (Chavez et al 2003, 2008). For the ecosystems the physical changes imply stress that is counteracted by the modification of their structures leading to higher transfer efficiency (Tam et al. 2008, Taylor et al. 2008a, b). Most obvious changes in both physic conditions and ecosystems states are associated with El Niño (EN), the warm extreme of the ENSO (e.g. Wolff et al. 2003, Bertrand et al. 2004, Swartzman et al. 2008, Ayón et al. 2008) that is thought to act as a “system reset” (Bakun & Broad 2003) and these changes are seen as rather short-term pertur-

bations (Csirke 1988, Muck 1989). Larger-scale oscillations with usually less extreme amplitudes and regime-like behaviour (“La Vieja” and “El Viejo”) lead to more persistent alterations of the ecosystems (Alheit & Bernal 1993, Hare & Mantua 2000, Alheit & Ñiquen 2004, Lluch-Belda et al. 1989, Chavez et al. 2003). Since the turn of the millennium a persistent cool regime has been observed in the northern HCS.

Numerous studies of the last century have empirically linked marine organisms to physical and biotic variables of their ecosystems but underlying mechanism have often not been determined. However, the existing examples and theoretical studies showed that such mechanisms are often multi-factorial and interacting in complex networks that usually do not allow lineal approaches (Stenseth et al. 2003, Keyl & Wolff 2008). Additionally, spatiality has shown to be an important feature that must be considered in future studies on the interaction of biota and their environment (Keyl & Wolff 2008, Argüelles et al. 2008, Keyl et al. 2008, *subm.*, in prep., Tafur et al. *subm.*).

Cephalopods are considered to be highly plastic in their ability to adjust to variable conditions of their environment (Boyle & Rodhouse 2005). This plasticity that mostly was restricted to growth-related parameters and reproduction was found to be dependent – again mostly empirically – of two main factors, one representing the physical and one the biological environment: water temperature and food availability (Mangold 1987). It can be assumed that the two factors are not independent, especially in areas like the HCS.

The reported change in size structure of mature females of *D. gigas* that occurred in 1999/2000 was tested for correlation to sea surface temperature anomalies (SSTA) of the northern HCS. Results found no relation (Argüelles et al. 2008) indicating a more complex interaction between size and environment. The triad hypothesis parted from these findings of a missing direct link between SSTA and size. It hypothesised the dependency of the biological response of *D. gigas* from its habitat and migration patterns through the different water masses of the HCS, that is, assumed spatiality of the interaction. The proposed triad of migration-maturation-growth reproduces the observed temporal population structures and predicted spatially different size structures (Keyl et al. 2008) that are confirmed by data from the Chinese fishery on jumbo squid outside the Peruvian EEZ (Ye & Chen 2007).

The mechanism for the adjustment to environmental variability is the high phenotypic plasticity of a number of morphological and life history traits. Analysis of data from the industrial jig fishery of *D. gigas* in the Peruvian EEZ identified a clear break in the states of the traits in 1999/2000 after the strong LN/EN of 1996 to 1998 (Argüelles et al. 2008, Keyl et al. subm., Tafur et al. 2008). In the Mexican Gulf of California, another important area for *D. gigas*, where usually large group of size-at-maturity is observed size alterations have also been found. There smaller specimens were found for almost three years during and after the EN-years (Markaida et al. 2004, Markaida 2006, Bazzino et al. 2007).

Biological traits that were found to be affected during and after 1999/2000 are mean size of the population, growth rates, longevity, terminal size, size-at-maturity and annual number of cohorts as well as reproduction processes becoming manifest in female:male-ratio, maturity and mated females and their temporal occurrence in the year. At the same time, abundance and the distribution range of *D. gigas* in the Eastern Pacific Ocean increased under a fishing regime that was higher than ever before (Argüelles et al. 2008, Tafur et al. subm., Keyl et al. subm., in prep.).

Life history and the individual biological traits that form its basis can be understood as strategy that defines how a species interacts with its environment (e.g. the classic example of r- and K-selection of Pianka 1970) and the concept usually includes constancy if considering a particular species. However, in well studied, exploited marine resources changes in the states of morphological and life history traits were observed and often are attributed to the directed, often size-specific impacts of fisheries that are even thought to become genetically assimilated (e.g. Hutchings & Baum 2005, Jorgensen et al. 2007). The present results indicate that the here observed changes in traits have to be considered to be environmentally induced as during the study period they occurred oppositely to what would have been expected if these changes had been induced by fisheries (Keyl et al. in prep.). Our results should therefore be considered as an important aspect in the assessment and management of other exploited populations. Additionally, effects of EV and fisheries on traits under certain conditions may be compensating each other what could lead to wrong and dangerous conclusions with respect to stock health and management measurements (Keyl et al. in prep.).

Jumbo squid, like other cephalopods, leads an energy demanding life in the “fast line” (Jackson & O’Dor 2001) and the present work proposes how this energy is acquired most efficiently and in case that the energy availability of the ecosystem is reduced how the demand is reduced as well. The governing factor of the observed temporal plasticity of biological traits of *D. gigas* as mentioned is the availability of energy in its habitats, that is, food availability and finally productivity of the ecosystem. This relates the different phenotypes of jumbo squid to spatially delimited areas determined by water masses as proposed by the triad hypothesis (Keyl et al. 2008, Keyl et al. in prep.). The synchronous alteration of biological traits as response to large scale modifications of the distribution of water masses before and after 1999/2000 led to the formulation of the hypothesis of the “energy optimization” strategy. This is the mechanism that allows *D. gigas* to optimize its energy use under energetically adverse and favourable conditions to cope with the full range of EV in its ecosystems in both hemispheres (Keyl et al. in prep.). It was proposed that it leads to a trade off where the two extremes correspond to population survival on one side and genetic diversification and the increase in individual fitness on the other (Keyl et al. 2008).

Additionally, three more features support the efficient use of the ingested food in general and help to understand why cephalopods can have gross efficiencies of up to 60%: (1) physiological characteristics that include protein-based metabolism, sustained growth, efficient handling of oxygen and reduced antioxidative defence (Jackson & O’dor 2001), (2) the population energy storage (Ibáñez & Keyl in press) and (3) the temporal decoupling of maturation processes (Tafur et al. subm.).

The population energy storage strategy bases in cannibalism and the evolutionary transfer of the individual energy storage to the population. It reduces energy loss related to the conversion of ingested proteins to storage metabolites and allows moving without motility handicap from individual storage organs (Ibáñez & Keyl in press, Keyl et al. in prep.). The decoupling of maturation of the two sexes distributes the energy required for reproductive tissues over a larger period by starting female maturation after the completion of the male maturation. In that way, it reduces the energy uptake rate and inter-sexual competition for resources. As immature females can store spermatophores, an additional effect of this strategy is the extension of the actual reproductive phase (Tafue et al. subm., Keyl et al. in prep.).

It is assumed that at least in *Dosidicus gigas*, if not in all cephalopods, all aspects of life history are completely subordinated to the optimized use of available energy. In that way they can survive under high variability and obtain the lead over ecological competitors.

The generally accepted hypothesis of the three groups of size-at-maturity of *D. gigas* proposed by Nesis (1970, 1983) under the light of the results of the here presented studies seems rather unlikely as is the potential genetic origin of these groups (Keyl et al. 2008, subm., in prep., Tafur et al. subm). However, a final falsification of the original hypothesis has to be supported by a future detailed genetic analysis.

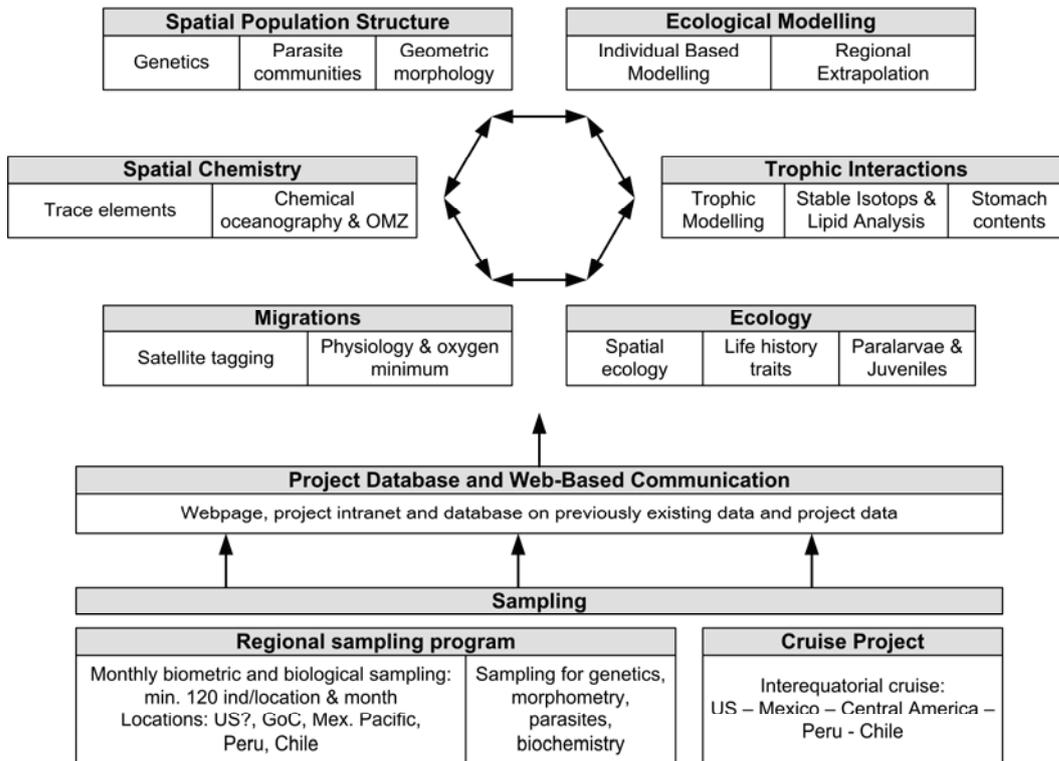
The results of the analyses of the present thesis that were mainly conducted on a temporal basis show the importance of spatial aspects and support the ideas of Keyl & Wolff (2008). Further work on the topic must be spatially explicit and use methods that are able to consider spatiality.

An important point that is considered crucial in the understanding of spatial effects on the life history of jumbo squid is its tolerance of hypoxic conditions (Gilly et al. 2006, Rosa & Seibel 2008). This tolerance considered under the light of the expanding minimum zones (OMZ) worldwide (Stramma et al. 2008) and the simultaneous range extension of *D. gigas* in the last decade has led to assumption that the habitat of jumbo squid depends on the OMZ (Gilly et al. 2006, Rosa & Seibel 2008). Contrary to other oceanic squids where migration patterns are well known, such patterns for *D. gigas* have not yet been confirmed and a deeper understanding of extension and connectivity of areas of reproduction and feeding does not exist.

The here presented studies examined the jumbos squid population of the HCS in the southern hemisphere only. Its results do not contradict the results of studies of the populations of the GoC and the Mexican Pacific. However, differences exist and future studies should have an “inter-equatorial” aspect to clarify to which extend our hypotheses are valid there. Until now, jumbo squid can not be hold in captivity for a time exceeding 12 days and hence it is difficult to directly test hypothesis that depend on physiology. A future project should therefore be multi-national and multi-disciplinary and comprise physiological, ecological, evolutionary, oceanographic and mathematical methods. A cen-

tral individual-based model could gather and spatially integrate data to overcome the problem of missing physiological knowledge and test the here proposed hypotheses. A possible outline for a future project is shown in Figure VI-1.

*D. gigas* is of importance for human populations that depend on artisanal fisheries especially in coastal areas in Peru and Mexico. Further research to understand dynamics of their resources in response to environmental variability will aid in the sustained use of the resources. The extreme response of *D. gigas* to its environment helped during the present studies to understand basic interactions but as a model it can also aid to identify and understand such links in the case of other marine resources.



**Figure VI-1: Possible structure of a multi-disciplinary project on *D. gigas* in both hemispheres of the Eastern Pacific Ocean.**

## CHAPTER VII: References

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**Erklärung nach §6, Abs. 5 der PromO vom 14. März 2007:**

Hiermit erkläre ich, dass ich

1. die Arbeit ohne unerlaubte fremde Hilfe angefertigt habe,
2. keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe und
3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Bremen, den 14. April 2009

A handwritten signature in blue ink, appearing to read 'F. Keyl', written in a cursive style.

Friedemann Keyl