

A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae)

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Abstract

The taxonomy, functional morphology, evolutionary biology and ecology of the jumbo squid, *Dosidicus gigas*, were reviewed using the data from many Soviet/Russian expeditions and all available literature. *D. gigas* is one of the largest and most abundant of the nektonic squid in the epipelagic zone of the world Ocean. It occurs in the eastern Pacific with its species range limited by the isoline of phosphate concentration of 0.8 mg-at P-PO₄³⁻/m² in the 0–100 m layer. Three intraspecific groups of *D. gigas* may be distinguished on the basis of the size of adult males and females: small (mantle length (ML) of adult males 130–260 mm, females 140–340 mm), medium-sized (240–420 and 280–600 mm, respectively) and large (>400–500 mm and 550–650 to 1000 mm and more, respectively). Growth is rapid. The life span of all three groups is about 1 year, with the biggest specimens of the large group probably living 2 years. *D. gigas* are monocyclic with the highest potential female fecundity among cephalopods; up to 32 million oocytes. Spawning takes place throughout the year, with a distinct peak during spring and summer in the southern hemisphere (October–January). *D. gigas* is an active predator. The most common prey among fish species are epipelagic lanternfish, and among squid species are ommastrephids, including *D. gigas*. Throughout the whole life cycle the prey sizes constitute 5–15% of the squid total length. Parasite fauna include 9–12 species of nematode, cestode and trematode, and the ciliate *Chromidina*. The total instantaneous stock of *D. gigas* within the limits of the species range was estimated at around 7–10 million tonnes, including around 2–4 million tonnes in the open ocean beyond the exclusive economic zones. © 2001 Published by Elsevier Science B.V.

Keywords: Jumbo squid; *Dosidicus gigas*; Distribution; Intraspecific structure; Ecology

1. Introduction

The jumbo squid, *Dosidicus gigas*, is the largest and one of the most abundant of the nektonic squid. It belongs to the family Ommastrephidae and the sub-family Ommastrephinae (Nesis, 1985). This squid

is distinguished from other ommastrephins by the structure of its species range, and by some important ecological traits (i.e. a complicated size structure, relatively weak sexual dimorphism in size, extremely high female fecundity etc.). The last review of *D. gigas* biology was published more than 15 years ago (Nesis, 1983), and since then new and important data on its biology and distribution have been collected. This was the main reason for the preparation of this short review of the basic biological features of *D. gigas*.

This report is only a brief sketch of the distribution and biology of *D. gigas*. Only the most important and

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fundamental data are presented, being significant (from the authors' point of view) for understanding the specific features of the biology of this unusually large squid.

2. Materials and methods

The present review is based on around 230 published papers on *D. gigas* biology. In addition, data were analysed from 46 Soviet and Russian expeditions (including 30 specialised cruises) carried out mainly in the exclusive economic zones (EEZs) of the Central and South American countries (between 14°N and 30–40°S and from the boundaries of the EEZs to 95–117°W) in 1965–1991. In 1984–1989, *D. gigas* resources were studied within the EEZ of Nicaragua. Overall, the cruise data include 3765 hydrological stations, 2090 light drifting stations, 1730 hauls by large pelagic rope trawls, 781 hauls by small pelagic trawls and 2368 plankton tows (mainly by Juday net).

From the plankton samples, 97 paralarvae were identified as *D. gigas*. 103 752 squid were measured and analysed. Age and growth were determined by processing and reading the statoliths of 113 squid (Arkhipkin, 1989; Arkhipkin and Murzov, 1986, 1987). The main reproductive parameters were investigated in 107 females (i.e. fecundity and the size distribution of oocytes in the ovary) and in 85 males (i.e. the number and sizes of spermatophores). The stomach contents of 1836 squid with full stomachs (including 750 stomachs with species identification and size re-construction of prey items) were examined; stomach indices were studied in 2978 specimens. Around 300 squid were kept in captivity to study the duration of food digestion. Helminths were analysed from 874 squid. Tissue samples of 750 *D. gigas* were studied by electrophoresis.

The abundance and biomass of squid at the light drifting stations were calculated after Zuev et al. (1985). Underwater observations of squid behaviour were made by scuba divers from an underwater anti-shark cage. The cage was designed by S.I. Bazanov (AtlantNIRO), and was the site of most of his underwater observations. The cage, which drifted near the ship was 1.5 m long, 1.6 m wide and 10 or 15 m high. The diver inside the cage observed squid from a

distance of up to 25–30 m. Underwater observations from the anti-shark cage were accompanied by squid counting from the ship to get a quantitative picture of their vertical distribution (i.e. the relation between the number of squid visible near the surface from the ship and their number in the upper 0–20 m water layer observed from the cage) for the zones of different squid abundance (Bazanov and Parfenjuk, 1986).

3. Results

3.1. Taxonomic and phylogenetic position

d'Orbigny (1835) first described the jumbo squid, *D. gigas*, as *Ommastrephes gigas* d'Orbigny, based on specimens collected in the southeastern Pacific. Later, Steenstrup (1857) introduced a new genus, *Dosidicus*, for his new species *Dosidicus eschrichtii* Steenstrup. Pfeffer (1912) synonymised *D. eschrichtii* with *D. gigas*, the latter as the senior synonym. At present the genus *Dosidicus* includes one extant species, *D. gigas* (d'Orbigny, 1835) (= *Ommastrephes giganteus* Gray, 1849; *D. eschrichtii* Steenstrup, 1857; *D. steenstrupi* Pfeffer, 1884) (Wormuth, 1976, 1998; Nesis, 1987), and one extinct species, *D. lomita* Clarke and Fitch, 1979, described by a statolith with a total length of 2.5 mm from the Late Pliocene Epoch of California (Clarke and Fitch, 1979).

D. gigas belongs to the subfamily Ommastrephinae, which is the most phylogenetically advanced subfamily of Ommastrephidae, but it is the least advanced member of this subfamily (Zuev et al., 1975; Nesis, 1979, 1985; Nigmatullin, 1979, 1988; Roeleveld, 1988). *D. gigas* is the largest ommastrephid squid, its dorsal mantle length (ML) is up to 1000–1200 mm and its weight up to 30–50 kg. In terms of many of the important morpho-functional features, i.e. in the development of the jet propelling system, fins, gladius, brain, statocysts, statoliths etc. (Arkhipkin and Murzov, 1986, 1987; Bizikov, 1996; Clarke and Maddock, 1988a,b; Young, 1988), this species has no substantial differences from the other four genera of Ommastrephinae (*Ommastrephes* d'Orbigny, 1835; *Sthenoteuthis* Verrill, 1880; *Eucleoteuthis* Berry, 1916; *Hyaloteuthis* Gray, 1849). All these squid are typical nektonic animals. *Dosidicus* is distinguished from the other four ommastrephins by the absence of large

mantle skin photophores (only minor photophores are present), by the absence of eye and intestinal photophores in paralarvae (which are present however in juveniles and subadults), and by elongated and attenuated arm ends. The arms of *D. gigas* have up to 200 pairs of suckers compared to not more than 32–35 pairs in other ommastrephin genera. The first two features (concerning photophores) are primitive features, while the third (attenuated arms), is an apomorphic feature.

The gladius is of a typical ommastrephin type and characterised by double marginal ribs on the rachis, long lateral plates, being arc-like bent on the short stem, and the drop-like callus of the hypostracum on the ventral side of cone flags (Bizikov, 1996).

3.2. The species range in evolutionary and ecological aspects

All Ommastrephinae have lost any connection with the seabed and the continental shelf regions, including at the time of reproduction. They are true pelagic squid that have mastered the open ocean of the tropical and temperate zones. However, despite its purely pelagic life style and spawning, *D. gigas* is the only member of the subfamily whose range does not spread from coast to coast and because of this its range is considered primitive in comparison with the other ommastrephin genera.

D. gigas occurs only within the eastern Pacific (Fig. 1). Its range is stretched meridionally and is semi-oceanic, while the ranges of the other ommastrephins are trans-oceanic and latitudinally stretched. *D. gigas* may be termed as an eastern Pacific tropical–subtropical nerito-oceanic species. The squid occur from 37–40°N (rarely to 44–45°N: E.M.C. Hatfield, pers. comm.) to 45–47°S, and are common between 30°N and 20–25°S. Within the equatorial area, the range is stretched westward as a strip, narrowing to the west and reaching 125–140°W (Nesis, 1983).

In general, the range of *D. gigas* lies within the neutral region of the current deformation field of the eastern Pacific, which is eutrophic throughout the year. The boundaries of its range pass along the eastern peripheries of the large-scale oceanic gyres of the central water masses and are approximately coincident with the isoline of the average phosphate concentration 0.8 mg-at $\text{P-PO}_4^{3-}/\text{m}^2$ in the 0–100 m

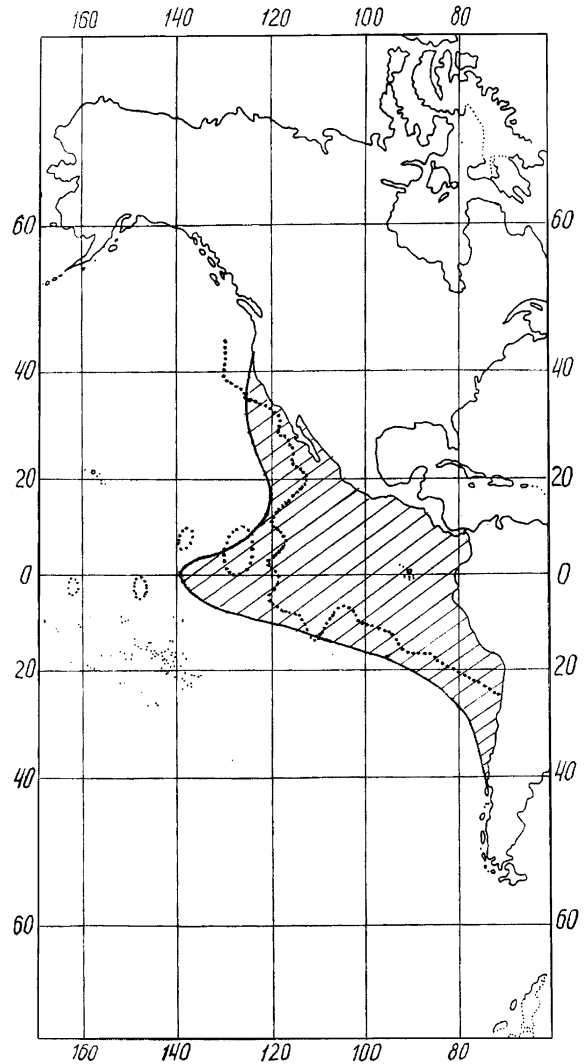


Fig. 1. The range of *D. gigas* (hatched area) and the isoline (···) of the year weighted mean phosphorus concentration of 0.8 mg-at $\text{P-PO}_4^{3-}/\text{m}^2$ in the 0–100 m layer (after Gershanovich et al., 1974).

layer (Aleksandronets et al., 1983) (Fig. 1). This isoline indicates the boundary of highly productive water (Gershanovich et al., 1974). The main habitats of *D. gigas* are transformed waters of the California and Peru currents and their derivatives.

The nerito-oceanic, or pseudo-oceanic, species range of *D. gigas* is not due to the peculiarities of its reproduction, as was suggested for example by Nesis (1970, 1983), but to its specialisation to life

within highly productive offshore communities with disbalanced production cycles (Nigmatullin, 1979, 1991; Aleksandronets et al., 1983). Dense concentrations of squid were observed in areas with a high oceanic potential energy, representing the areas of high plankton concentration.

The reproductive part of the species range is located between 25°N and 20–25°S, mostly not further than 50–150 nm from the shore. However, between 10°N and 15–20°S it stretches to 200–450 nm offshore. The main spawning areas are situated over the continental slope and in adjacent oceanic waters, while the feeding grounds of immature squid are predominantly further offshore.

3.3. Intraspecific structure

The intraspecific structure of *D. gigas* is complicated, as is the case for many other ommastrephids. There are many local, sometimes allopatric but mostly sympatric and parapatric, groups, which differ from each other in many important ecological aspects. Three groups may be distinguished on the basis of the size (ML) of adult males and females: a small group (130–260 mm and 140–340 mm, respectively), a medium-sized group (240–420 mm and 280–600 mm, respectively) and a large group (>400–500 mm and 550–650 to 1000–1200 mm, respectively).

The ranges of both the small- and medium-sized groups fully or partially overlap, as do the ranges of the medium-sized and large-sized groups. Squid of the small-sized group are found predominantly in the near-equatorial area, those of the medium-sized group live within the whole species range (except in the most high-latitude parts) and those of the large-sized group occur at the northern and southern peripheries of the range (usually northward of 10–15°N and southward of 10–15°S). However, large squid sometimes reach as far as the equator, in association with intrusions of the nearshore cold currents, mostly the coastal branch of Peruvian current coming from the south.

In general, *D. gigas* is in the process of intensive adaptive radiation. Thus it is possible that these groups, in which genetic differentiation is unknown, are in fact well separated from each other and represent species *in status nascendi*, or at least different population systems (=stock units).

3.4. Vertical distribution

D. gigas is a pelagic species inhabiting the areas offshore of the continental shelves, from the surface to depths of at least 1200 m. Squid are occasionally found over the shelves and near shores during feeding migrations. Adult squid (>150–180 mm ML) undergo diel vertical migrations with a night lift to the 0–200 m water layer, plunging in the daytime to 800–1000 m and deeper (Yatsu et al., 1999b). Its upper temperature limits range from 15 to 28°C in surface waters, and even 30–32°C in equatorial areas, while its lower temperature limits are not less than 4.0–4.5°C in the deeper water. During the day, squid stay within or just below the layer of the deep oxygen minimum.

3.5. Horizontal migrations

Horizontal migrations may be passive (i.e. the drifting of egg masses, larvae and juveniles, and sometimes even adults, with the currents) or active (adults). The massive feeding migrations of growing squid occur in the austral summer and autumn. Squid migrating from their feeding areas to their spawning areas form large and dense schools comprising thousands of animals and move with a speed ranging from 5–10 to 20–25 km/h (Nesis, 1970; Sabirov, 1983).

Squid migrate from the Pacific Ocean to the Gulf of California, moving northward and northwestward during winter and spring, reaching 28–29°N, and in the opposite direction during summer and autumn (Klett, 1981; Ehrhardt et al., 1983a,b, 1986). Irregular seasonal invasions of migrating squid into coastal areas both in the northern (western USA) and southern (central Chile) peripheries of the species range are mainly the result of active feeding migrations in the years of high abundance (see Nesis, 1983 for a review of the old data). The last increase in abundance and intrusion into central Chilean waters was observed at the beginning of the 1990s (Schmiede and Acuna, 1992) and at the northern periphery of the range (western USA) during 1998 and 1999 (F.G. Hochberg and U. Marcaida, pers. comm.).

3.6. Age and growth

Age and growth of *D. gigas* have been studied using two different methods, i.e. cohort analysis using length–frequency distributions (Ehrhardt et al.,

1983a,b) and ageing analysis using statolith and gladii techniques (Arkhipkin and Murzov, 1987; Bizikov, 1996; Masuda et al., 1998). Cohort analysis has revealed five cohorts with different hatching times. Squid of each cohort had their own type of growth curves, which were fitted either by the linear function or the von Bertalanffy function. Absolute growth rates were high during the first four months of life (ranging from 65 to 83 mm per month), but then decreased to 36–56 mm per month in squid of 8–10 months in age. It was suggested that squid could attain 700–750 mm ML by the age of 1 year (Ehrhardt et al., 1983a).

Statolith ageing studies generally confirmed the high growth rates of *D. gigas* revealed by cohort analysis. Squid can attain large sizes in less than 1 year. For example, a maturing female of 720 mm ML had 345 growth increments in its statoliths (Arkhipkin, 1989), a 770 mm ML male and a 860 mm ML female had 352 and 338 growth increments, respectively (Masuda et al., 1998). Statolith growth increments have not yet been validated for this species, however if the hypothesis ‘one increment — one day’ is true for *D. gigas* then it has an annual life cycle, as have many of the other ommastrephid squid (Arkhipkin, 1989).

Growth is fast at paralarval and juvenile ontogenetic phases, ranging from 5 to 8% ML per day. It is notable that *D. gigas* is characterised by the highest juvenile growth rates of all the ommastrephids, enabling them to attain 100–110 mm ML by 45–55 days old. In immature adult squid however, growth rates decrease to 0.8–1.5% per day, which are relatively common growth rates for the other ommastrephids (Arkhipkin, 1989). Mature squid also grow, but with slow growth rates (0.2–0.4% per day). Growth in the adult phase can be approximated by linear function (Arkhipkin and Murzov, 1987; Masuda et al., 1998). Squid hatched in different seasons have different growth rates. The highest growth rates were observed in the winter-hatched group (August–September), the lowest in the summer/autumn-hatched group (February–May) (Masuda et al., 1998).

Independent studies of *D. gigas* growth rate by the gladii ageing techniques revealed the exponential growth of females (ML ranging from 22 to 492 mm) and slightly sigmoid growth in males (ML ranging from 10 to 272 mm). It was shown that females grow up to 490 mm ML in 12.8 months, whereas males grow up to 260 mm in 11.5 months.

The longevity of all three groups of *D. gigas* is therefore about 1 year, but some huge specimens (>750 mm ML) of the large group can live for longer (up to 1.5–2 years, Arkhipkin, unpublished data).

3.7. Reproduction

D. gigas is monocyclic and so individual squid have only one reproductive season during their life. The potential fecundity of large females is the largest recorded of all the cephalopods; up to 32 million oocytes (Nigmatullin et al., 1999). However, the potential fecundity generally varies between 0.3 and 13 million. The proportion of vitelline oocytes and mature eggs in the ovary and oviducts of pre-spawning females usually constitutes about 10% of the potential fecundity. The number of spermatophores varies between 300 and 1200 and their size is ~25–35 mm.

Reproduction is all year round with a peak in spawning during spring and summer in the southern hemisphere (October–January). Spawning takes place both over the continental slope and in adjacent oceanic areas. Mating is in the head-to-head position; spermatophores are placed on the buccal membrane of a female. Eggs are oval with a maximum diameter of 0.8–1.0 mm. Spawning presumably takes place in the near-surface water layer, but egg masses are unknown. Individual spawning periods should be long and intermittent (batch spawning).

Mating was only observed once at a night light station while the ship was drifting. A male (~220 mm ML) swam slowly near a female (~350 mm ML) for around 20 s. The male then approached the female and both animals interweaved arms in the head-to-head position, gently moving their fins. This lasted for approximately 50 s and then the squid separated (Parfenjuk, pers. comm.).

Embryonic development lasts for 6–9 days at 18°C. The ML at hatching averages 1.1 mm (Yatsu et al., 1999a). The paralarva is a typical rhynchoteuthion. They inhabit the upper water layers (mainly 0–100 m). Ontogenesis includes the following phases: paralarva (1–10 mm ML), juvenile (15–100 mm ML), subadult (150 to 300–350 mm ML) and adult (400–1000 mm ML), and with three transient periods: at ML 10–15 mm, at 100–150 mm and from 300–350 to ~400–450 mm. During these periods, the morphology, food spectrum and ecological status of the squid change

(Nigmatullin, 1987a; Arkhipkin and Murzov, 1987; Shchetinnikov, 1989). The eye photophores and two intestinal photophores are absent in paralarvae and adults. However, they develop in the juvenile phase at approximately 12–15 mm ML and disappear at 100–140 mm ML (Nigmatullin and Dubinina, unpublished data; Shchetinnikov, 1987). The light of all photophores (including minute skin photophores) is blue-green.

3.8. Food and feeding

D. gigas is an active predator, pursuing its prey. The common prey species are copepods, hyperiid amphipods, euphausiids, pelagic shrimps and red crabs (*Pleuroncodes planipes*), heteropod molluscs, squid, pelagic octopods and various fishes. The feeding spectrum changes continually with predator growth, from macroplanktonic invertebrates and fish fry (in *D. gigas* juveniles) to fish and squid (in adults). Near-surface lanternfish completely predominate among fish prey. They are the most common food items for even the largest squids (500–800 mm ML), while the ommastrephids, including *D. gigas*, were predominant among squid prey. During ontogenesis, the relative size of prey items remains the same, being 5–15% of the total length of the predator (Shchetinnikov, 1986, 1988). The large form of *D. gigas* (>500–600 mm ML) also feed on relatively small-sized, but abundant and aggregated fishes, mainly myctophids (Marcaida, pers. comm.). Feeding is most active at dusk and dawn, but many squid feed throughout the night.

Cannibalism is common, but only a relatively small number of juvenile squid (3–4%) are eaten by squid of the same species. However, cannibalism was much greater in the light field near the ship. In the Gulf of California, cannibalism may account for as much as 30% by weight of the diet of *D. gigas* in months when common prey items are scarce (Ehrhardt, 1991). The daily rations of adult squid (200–350 mm ML), according to experimental work and field observations, range from 5 to 9% of body weight (Bazanov, 1987a; Shchetinnikov, 1988).

3.9. Biotic relations, behaviour, predators and parasites

The muscles and collagen tunic of the mantle, funnel and fins, as well as the brain, are well-devel-

oped, and so *D. gigas* is among the most advanced of the nektonic squid (Zuev, 1975; Nesis, 1983, 1987). Behaviour has been studied mainly during light drift stations and by scuba divers (Bazanov, 1987a,b,c, 1988; Bazanov and Parfenjuk, 1986; Nigmatullin, 1987b; Parfenjuk, 1987; Parfenjuk et al., 1983; Sabirov, 1983). Juvenile *D. gigas* are the most active of the ontogenetic phases. They occur in small schools (20–40 animals) between the surface and upper isothermal layer (20–50 m) (Parfenjuk, 1987). They sometimes move at high speed and may even fly out of the water (Cole and Gilbert, 1970; Bazanov and Parfenjuk, pers. comm.). Subadults are usually less active than juveniles. They chase their prey both individually and in groups. Subadults aggregate into hunting schools of 20–200 individuals, with a maximum of 100–1200 individuals (Bazanov, 1987a,b,c; Parfenjuk, 1987; Parfenjuk et al., 1983). They move with speeds from 5–10 to 20–25 km/h (Sabirov, 1983). Schools of adults are even less abundant with 2–5 to 10–12 animals (Bazanov, 1987c; Parfenjuk, 1987). Large adult squid are opportunistic predators, preying mainly upon lanternfish. However, they are sometimes aggressive; Hall (1990) describes an aggressive attack by a large *D. gigas* on a scuba diver.

Interspecific competition between *D. gigas* and other cohabitant ommastrephid squid may be acute. The food spectra overlap extensively for the middle-sized *D. gigas* and the large *Sthenoteuthis oualaniensis*, their distribution ranges also strongly overlap. For *D. gigas* and *Ommastrephes bartramii*, the distribution ranges and food spectra overlap to a much lesser degree. Competition for food is decreased by different areas having high concentrations of different squid species (*S. oualaniensis* prefer warmer waters than *D. gigas*), by different patterns in their vertical distribution (at night *D. gigas* occur at shallower depths than *S. oualaniensis* and adult *D. gigas* occur at shallower depths than subadults) and by different hunting times in squid of different sizes (Bazanov, 1987a,b,c; Bazanov and Parfenjuk, 1986). Despite possible food competition, *D. gigas* and *S. oualaniensis* commonly form mixed schools (Bazanov, 1987c; Shchetinnikov, 1988).

Predators of *D. gigas* are numerous and differ in size and ecological characteristics. Juveniles are preyed upon by juveniles of large carnivorous fishes, small tunas, squid (*S. oualaniensis*) and gulls etc.;

subadults (150–250 mm) by dorado (*Coryphaena hippurus*), snake mackerel (*Gempylus serpens*), yellowfin tuna (*Thunnus albacares*), other large tunas, and fur seals; and adults by large sharks, swordfish (*Xiphias gladius*), striped marlin (*Tetrapturus audax*), sperm whales and pilot whales.

The parasite fauna include 9–12 species of nematode, cestode and trematode and the ciliate *Chromidina*. All parasitic worms affect the larval stages of squid, and they all have a wide host specificity. *D. gigas* is therefore one of the paratenic hosts (Gaevs-kaya et al., 1982, 1983; Shukhgalter, 1988; Shukhgalter and Nigmatullin, 2001).

During its ontogenesis, *D. gigas* occupies successively sub-niches of micronektonic planktophage — consumers of the II–III level of the food chain and of small and medium-sized predators — consumers of the III–V (usually IV) level of the food chain — in the pelagic ecosystems of the eastern Pacific. It is one of the keystone species participating in the biological transfer of energy from the macroplankton and plankton-eating fish to the largest pelagic predators — consumers of the V–VII level of the food chain (Shchetinnikov, 1988).

3.10. Abundance

Inter-annual changes in abundance, size range, composition and quantitative relations within the three groups of *D. gigas* are considerable. Squid are larger and mature later during the periods of strong trade winds than during a slackening of the Peruvian upwelling. In warm years (El-Niño and El-Aguaje), the large-sized group decreases in abundance and the squid are driven into nearshore areas, whereas the small- and medium-sized groups became more common. For example, in 1965–1968 (both El-Niño and El-Aguaje were simultaneously observed between September 1965 and January 1966, while in 1967–1968 temperatures were close to the annual average) large squid of 500–1100 mm ML predominated in the open waters of Peru (Baral, 1967; Nesis, 1970; Shevtsov, 1970). At other times, large *D. gigas* are absent from that area with only small- and (more commonly) medium-sized squid (<500–550 mm ML) present (Nigmatullin et al., 1991; Tafur and Rabí, 1997). The reason for the occurrence of large squid in the open ocean is mainly due to changes in water circula-

tion and the consequent restructuring of the oceanic ecosystems (Nigmatullin et al., 1991).

Biomass estimates for *D. gigas* have been made for the Gulf of California and the Pacific Ocean off the Gulf of California (Klett, 1981; Ehrhardt et al., 1983a,b, 1986; Hernández-Herrera et al., 1998), for the EEZ of Nicaragua (Nigmatullin, 1999), for the zone of Costa Rican upwelling (Froerman and Zheronkin, 1990) and for open areas of the equatorial and Peru regions (Nigmatullin and Parfenjuk, 1988; Nigmatullin et al., 1991). In the open waters of Peru (5–20°S and west of 95°W to the boundary of the EEZ; 1.01–1.21 million square kilometre) in 1982, the biomass of *D. gigas* was estimated at 820–1620 thousand tonnes, including 175–1250 thousand tonnes in dense aggregations (Nigmatullin et al., 1991). In the equatorial zone (0.12 million square kilometre, 1°N–1°S, 95–106°W) during 1981–1983, the biomass of *D. gigas* was estimated at around 90–150 thousand tonnes (Nigmatullin and Parfenjuk, 1988). Within the EEZ of Nicaragua, the biomass was estimated to vary from 12 to 275 thousand tonnes in 1984 to 1986 (Nigmatullin, 1999). In the open waters of Nicaragua and Costa Rica (8°00′–10°10′N, 89°20′–92°30′W), in the area of the Costa Rica upwelling (58.9 thousand square kilometre), the total biomass of *D. gigas* was estimated at 1114 thousand tonnes in June 1990 and 825 thousand tonnes in July 1990 (Froerman and Zheronkin, 1990 and pers. comm.). The biomass of *D. gigas* in the Gulf of California was estimated between 34.9 and 65.6 thousand tonnes in May 1996 (May is the month of new recruitment to the fishery, the data were collected in October 1996) (Hernández-Herrera et al., 1998), while off Sonora State it was estimated at 63.7–97.9 thousand tonnes in 1995 (Morales-Bojórquez et al., 1997) and 31 thousand tonnes in May 1996 (Solís-Nava and García-Badillo, 1996). The biomass of *D. gigas* was estimated at 210 thousand tonnes within the Mexican Pacific EEZ off the western Gulf of California peninsula in 1989–1991 (Sanchez-Juarez, 1991; De la Rosa et al., 1992).

The total instantaneous stock of *D. gigas* within the species range is estimated at around 7–10 million tonnes, including around 2–4 million tonnes in the open ocean beyond the EEZs. Approximately 1.0–1.5 million tonnes of squid occur in aggregations. Supposing a daily intake of 7% body weight (Bazanov,

1987a), then the total stock of squid of >150–200 mm ML may consume 0.5–0.7 million tonnes of food per day and around 200–250 million tonnes per year. Ehrhardt (1991) estimates that *D. gigas* may have consumed 60 thousand tonnes of food during their 9-month stay in the Gulf of California. Of course, these are only rough estimates reflecting the order of magnitude.

4. Discussion

The jumbo squid, *D. gigas*, belongs to the group of large squid of the subfamily Ommastrephinae, which also includes *Ommastrephes* (the only species being *O. bartramii*) and *Sthenoteuthis* (currently two species, *S. pteropus* and *S. oualaniensis*). In the phylogenetic hierarchy its place is closer to *Ommastrephes* than to *Sthenoteuthis* (Nesis, 1979, 1985; Nigmatullin, 1979, 1988). As is the case for *O. bartramii*, *D. gigas* has no large skin photophores and no photophores in the late paralarvae, but in contrast to *O. bartramii* it has temporarily developed photophores on the eyes and gut. *Sthenoteuthis* have constant eye and gut photophores and large skin photophores on the dorsal side of the mantle (except the dwarf form of *S. oualaniensis*). All three genera and four species have an oceanic distribution and (again except the dwarf form of *S. oualaniensis*) are more or less of large size. Other, more advanced members of the Ommastrephinae, *Eucoleoteuthis luminosa* and *Hyaloteuthis pelagica*, have a more sophisticated photophore system, are of smaller size and have different types of range (Zuev et al., 1975; Nesis, 1985; Nigmatullin, 1979, 1988).

The evolution of *Dosidicus*, *Ommastrephes* and *Sthenoteuthis* was governed by the competition for ecological dominance among the large squids conquering the epipelagic layer of the ocean (Nesis, 1985). *D. gigas* differs from the other species of this group in that it was unable to master the open ocean far from nearshore areas. The cause probably lay in its large size and rapid growth, both of which tied this species to highly productive areas only. However, in these areas it can fully out compete other ommastrephids. *O. bartrami*, *Todarodes filippovae*, *E. luminosa* almost never enter areas where *D. gigas* is common. Only *S. oualaniensis* may cohabit with *D. gigas*,

although this is mostly outside the range of the large-sized group.

D. gigas, in common with other large ommastrephids, has rapid, avalanche-like ovary maturation, protracted intermittent (multiportional) spawning, not associated with the bottom, and non-interrupted feeding and growth in the reproductive period. However, it differs from other large ommastrephids by the absence of pronounced sexual dimorphism in the size of adults and by its immense potential fecundity (Nigmatullin and Laptikhovsky, 1994). Its intraspecific structure is more complex than that of *Ommastrephes* but is comparable to that of *Sthenoteuthis*, probably the most complex of all cephalopods (Zuev et al., 1985; Nesis, 1993). Nevertheless, all groups, despite differences in adult size, demonstrate rapid growth, short life cycles and pronounced r-strategy. The ability to catch prey of quite a wide size range and to consume relatively small but common and aggregated prey, even in the adult phase, enables *D. gigas* to dominate within the pelagic ecosystems of the eastern Pacific.

The number of unresolved points in the study of *D. gigas* is endless, as for every other scientific problem. However, three of these are particularly important in relation to a proper understanding and the rational management of exploited stocks.

1. Over the last 35 years, *D. gigas* has been studied by several American countries (Mexico, Peru, Ecuador etc.) and by Japan exclusively within the EEZs, whereas the USSR undertook their research outside the EEZs (except for those of Peru and Chile in the 1960s and Nicaragua in the 1980s). Thus, the squid have been studied in different areas, at different times and by different methods. It is therefore impossible to pool all the existing information to provide a complete picture. As a result, we cannot understand the reasons for the sudden appearance of large squid in certain areas and their subsequent disappearance from these areas for many years. It is necessary to conduct joint expeditions in both nearshore and offshore areas using similar methodologies. This will be expensive but is both necessary and possible.
2. We do not know the taxonomic status of the three size groups. Are they parts of a single stock, as stated for the stock of the Gulf of California

(Klett, 1981; Ehrhardt et al., 1983a,b, 1986; Hernández-Herrera et al., 1998), or are they genetically different and belonging to different stock units? The latter, we assume, is more probable. The problem may be resolved by genetic studies.

- Two methods were used to study the age and growth of *D. gigas*: statolith ageing techniques (Arkhipkin, 1989; Arkhipkin and Murzov, 1986, 1987) and the gladius method (Bizikov, 1996). The results are similar in general but differ in detail. Construction of a general growth model is important for modelling the dynamics of exploited populations.

Acknowledgements

We would like to thank C. Yamashiro and M. Rabí (Instituto del Mar del Peru) for inviting and financially supporting our participation at the International Symposium on Pacific squids (Trujillo, Peru, October 1999). We are grateful to U. Marcaida, F.G. Hochberg, Y.M. Froerman and Y.N. Zheronkin for providing unpublished data. This study was supported in part by the Russian Foundation for Basic Research, project No. 00-05-64109 (ChN, KN).

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