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Reconstruction of the feeding activity of marine top-predators foraging at sea

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Abstract : Top-predators in the Southern Ocean consume large quantities of marine resources and therefore, interact significantly with human fisheries. Thus, collection of information on seabird and marine mammal feeding activity is of prime importance but their behaviour at sea cannot be assessed directly. Consequently, over the last three decades researchers have attached micro-data recorders to marine predators. These units monitor various parameters as a function of time. The measurement of the feeding activity of seabirds and marine mammals while at sea has evolved from indirect to direct methods, the latest consisting of monitoring the internal temperature of these predators. Recently, substantial progresses were made when temperature was recorded in the upper part of the oesophagus of seabirds in tandem with the recording of other parameters. After a brief review of the various methods to determine the feeding activity of top-predators at sea, this article will discuss the results and potential of internal temperature recorders with a special emphasis on oesophageal temperature recorders-for determining the foraging behaviour of seabirds and marine mammals.

Key words : oesophageal temperature, feeding activity, loggers, top-predators

1. Investigating the feeding activity of marine animals: a key parameter to the management of marine resources.

Among the abundant fauna of top-predators exploiting the Southern Ocean, seabirds are the largest by number (CROXALL, 1984; CROXALL *et al.*, 1984), with penguins representing up to 90% of the bird biomass in the Antarctic regions (MOUGIN and PREVOST, 1980). In addition, both marine mammals and seabirds consume key species in the trophic chains of this ecosystem, which makes them potential competitors with human fisheries (FURNESS, 1990; FURNESS and COOPER, 1982). Over recent years, conflicts between fisheries and ecologists have sometimes resulted in controversial measures. Although "culls", consisting of the removal of predators in order to optimize the development of prey stocks for fisheries, have been apparently successful in some instances, the underlying effects of organism removal is still incompletely controlled due to the complexity of trophic chains (see YODZIS, 2001). Thus, an understanding of the feeding ecology and the food require-

ments of marine top-predators is of prime importance. Using these predators as bio-indicators of marine resources (*e.g.* CROXALL *et al.*, 1988; FURNESS and NETTLESHIP, 1990) could help improve conservation and management of both the seabird community (HUNT, 1991) and the stocks of the marine resources (CCAMLR, 1986; CROXALL *et al.*, 1988).

In this respect, studies on the feeding behaviour of seabirds and marine mammals at sea have flourished despite the difficulty of directly observing the animal foraging in its natural environment: Although seabirds and marine mammals need to replenish regularly their oxygen reserves at the water surface, a large component, if not all (in the case of penguins or seals), of their foraging activity takes place underwater. In the early eighties, progress in the micro-chip technology branch was applied to marine biology and opened a new area of science where the activity of animals in an inaccessible environment could be monitored by devices collecting time-series data (KOOYMAN and DAVIS, 1982; Le BOEUF *et al.*, 1988; NAITO *et al.*, 1990). These devices, termed loggers, are attached to animals departing for a

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foraging trip and are recovered when the animals return to land to feed their offspring. Thanks to this technology, several insights in the "hidden" life of marine top-predators have been highlighted (*e.g.* WILSON, 1992; Le MAHO, 1994). Earlier pioneer works demonstrated the unexpected diving capacities of seabirds and marine mammals (KOOYMAN, 1989) and researchers have become aware of the large volume of water column that these animals can exploit.

However, despite an intensive use of loggers over the past three decades, the timing of prey intake, the amount of food ingested and the prey pursuit and capture by good marine top-predators remain poorly understood. These parameters are extremely difficult to monitor and are in most of the case, estimated by indirect means. In this article, we wish to review briefly the different methods for determining the feeding activity of marine top-predators, with special emphasis on recent studies that involve recording the internal temperature in the upper part of the digestive system of seabirds (ANCEL *et al.*, 1997; ROPERT-COUDERT *et al.*, 2000 a; 2001a). In this regard, the accuracy of oesophageal temperature logger for detecting prey ingestion (especially in penguins), as well as estimating the amount of food ingested and the prey species ingested, will be discussed below. Finally, the potential of internal temperature recording for ecological studies concerning foraging strategies resulting in optimized prey detection and capture will be highlighted.

2. Indirect information about the feeding behaviour

Because visual observations of marine animals feeding close to the shore (*e.g.* WILSON, 1996) or from boats (KOOYMAN, 1975; KOOYMAN *et al.*, 1971) are few and the amount of information collected is necessarily restricted, the feeding activity of animals have often been discussed based on indirect information. Two examples of investigations of the feeding behaviour through indirect evidence are discussed below:

1-Where do top-predators feed? This question can be envisaged from two point of views, the horizontal (latitudinal and longitudinal)

and vertical (depth zone in the water column) point of view. From an horizontal point of view, the preferred foraging grounds of animals at sea have been extensively investigated using remote-sensing methods such as satellite telemetry (WEIMERSKIRCH and WILSON, 1992; BOST *et al.*, 1997; KERRY *et al.*, 1995) or using loggers attached on the animals that record, for instance, the heading and swim speed in order to reconstruct the route taken by animals (see WILSON and WILSON, 1988). These studies showed that top-predators can travel astonishing distances at sea, flying up to 15,000 km (as is the case for the Wandering albatross, *Diomedea exulans*, JOUVENTIN and WEIMERSKIRCH, 1990) or swimming regularly 400–600 km from their colony (in the case of King penguins, *Aptenodytes patagonicus*, BOST *et al.*, 1997). After adopting a straight course to bring them to a foraging site, top-predators generally remain in specific areas where they concentrate their diving activity, revealing in this the location of their favorite food resources (BOST *et al.*, 1997; BORNEMANN *et al.*, 2000; PÜTZ *et al.*, 2000). In the Southern Ocean, these preferred feeding zones have been often shown to coincide with marine frontal structures where upwelling movements of water result in enhanced primary, and consequently, secondary and tertiary production (TYNAN, 1998). Substantial information on the status of a given ecosystem can be obtained when the preferred foraging grounds of top-predators can be directly correlated with prey availability (WEIMERSKIRCH *et al.*, 1994; BOYD *et al.*, 1994; KITAYSKY *et al.*, 2000; WIENECKE *et al.*, 2000; RODHOUSE *et al.*, 2000).

Among marine top-predators, marine mammals and a large proportion of seabirds prospect an important proportion of the water column, down to 500 m (in the case of emperor penguin, *Aptenodytes forsterii*, KOOYMAN and KOOYMAN, 1995) or 600 m (in the case of Northern Elephant seals, *Mirounga augustirostris*, Le BOEUF *et al.*, 1988). Thus, studies about preferred foraging grounds of such deep diving species, should take into account their vertical distribution. Therefore, among the various parameters recorded by loggers over the past decades, diving depth recordings have revealed

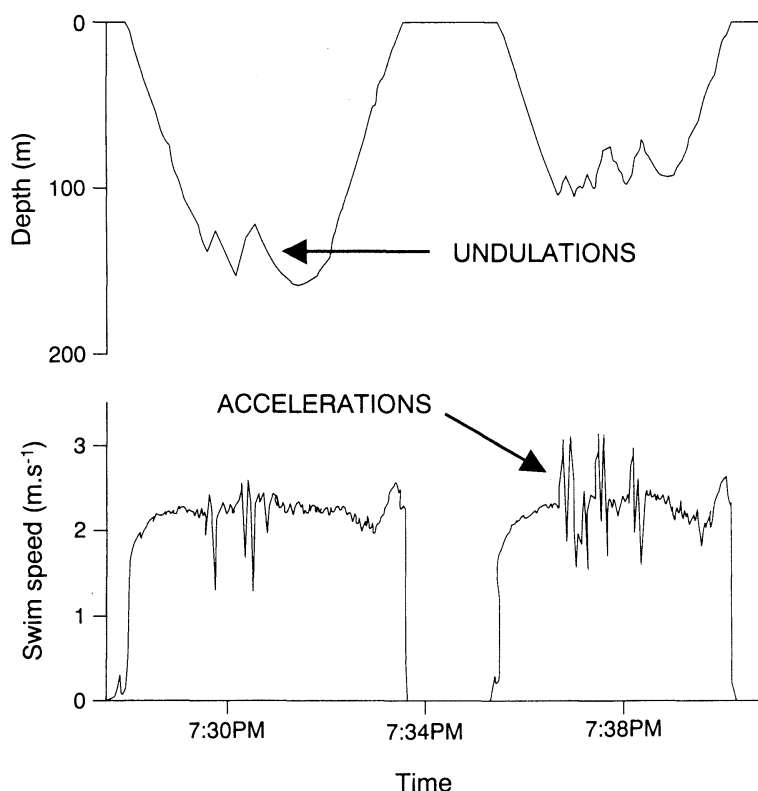


Fig. 1. Dive depth and swim speed recorded as a function of time in a free-ranging King penguin, *Aptenodytes patagonicus*. Arrows indicate undulations in the bottom part of the depth profile (top graph) and accelerations observed in the swim speed profiles (bottom graph) that are thought to represent prey pursuit.

the depth where prey are caught (WILSON, 1989; SEDDON and VAN HEEZIK, 1990; WANLESS *et al.*, 1993). Moreover, analysis of the diving depth of marine animals gives indirect indications on the feeding behaviour, for example, using abrupt changes in depth – sometimes termed undulations, wiggles or zigzags – observed at the bottom part of the depth profile of diving seabirds (*e.g.* WILSON, 1995), as indicators of prey pursuit. On a finer scale, drastic accelerations recorded during swimming by King penguins are believed to represent active pursuit of prey and, as such, an indicator of feeding activity (Fig. 1, see ROPERT-COUDERT *et al.*, 2000b for details). However, it is necessary to confirm that a pursued prey is actually ingested. Moreover, although the capture speed displayed by predators is related to prey escape speed (WILSON and ROPERT-COUDERT, sub-

mitted), information on the species and amount captured are not provided by these types of data.

2-What do top-predators consume? In parallel with the location of animals at sea, the assessment of the diet composition of marine seabirds and mammals has evolved from *post-mortem* analysis of the stomach contents, feces and pellet identification (See review in FURNESS and MONAGHAN, 1987; see also JACKSON and DUFFY, 1984), to the recovery of the stomach contents by non-mortal pumping and flushing methods (EMISON, 1968; DAHLGREN, 1982; WILSON, 1984). The evolution of the diet within individuals (*e.g.* KATO *et al.*, 1996) and /or during the breeding season (ADAMS and KLAGES, 1987; RIDOUX and OFFREDO, 1989) has helped highlight depletion in certain marine stocks (CROXALL *et al.*, 1999; IRVINE *et al.*, 2000)

or environmental fluctuations (AINLEY *et al.*, 1998). However, all of these methods are subject to bias (see BEDARD, 1976; CROXALL and PRINCE, 1980; CARSS *et al.*, 1995), especially since a portion of the food ingested is digested while animals are at sea (WILSON *et al.*, 1989). Differential digestion, examined in the Jackass penguin, *Spheniscus demersus* (WILSON *et al.*, 1985; WILSON *et al.*, 1989) may lead to an underestimation of the amount of food ingested or the preferred prey type. In seals, the accumulation of prey remains adds to the difficulty of an accurate estimate of the food consumption (see GALES and RENOUF, 1993).

The necessity of relating the location of the animals at sea to the type and amount of prey captured, as well as the incomplete information brought by collection of stomach contents, has meant that the direct measurement of the food intake of free-ranging animals is a particular challenge to researchers.

3. Direct recording of the feeding activity: internal temperature loggers.

Since most of the top-predators in the Southern Ocean are endotherms – *i.e.* maintain a high internal temperature independent of ambient temperature – the recent monitoring of the internal temperature of predators has revealed much about feeding habits (see BENGSTON, 1993; *e.g.* GALES and RENOUF, 1993; HEDD *et al.*, 1996; WILSON *et al.*, 1992), because these endotherms ingest mainly ectothermic prey (*i.e.* body temperature \approx water temperature) which cause precipitous drops in the predator stomach temperature (WILSON and CULIK, 1991; WILSON *et al.*, 1992). In addition to feeding behaviour studies, the physiological adaptations to diving of marine mammals and birds has been investigated in a number of studies based on the principle of internal temperature recordings (HANDRICH *et al.*, 1997; WILSON and CULIK, 1991).

Temperature has been primarily monitored in the stomach of a variety of marine mammals and birds (KATO *et al.*, 1996; PÜTZ, 1994; PÜTZ, and BOST, 1994; WEIMERSKIRCH and WILSON, 1992; WILSON, and CULIK, 1991; WILSON, *et al.*, 1992; 1998). In such studies, animals were induced to swallow stomach temperature

loggers, which are generally cylindrical devices built into an inert metal housing to resist digestive acids. One or two thermistors at the extremities of the device record the temperature. However, when placed in the stomach, several factors tended to decrease the efficiency of the loggers in detecting prey ingestion over time since the stomach fills and prey items may cover the sensor (see review in GRÉMILLET and PLÖS, 1994; WILSON *et al.*, 1995). In addition, the likelihood of detecting ingested prey depends on the position of the logger inside of the stomach (GRÉMILLET and PLÖS, 1994; WILSON *et al.*, 1995b) because body temperatures of diving seabirds may also fluctuate independent of feeding activity (*e.g.* BEVAN *et al.*, 1997; CULIK *et al.*, 1996; HANDRICH *et al.*, 1997; WILSON and GRÉMILLET, 1996). For example, if the sensor is in direct contact with the stomach wall, the temperature recorded can remain constant, or vary little, even when prey are ingested (ROPERT-COUDERT *et al.*, 2000a).

Recently the monitoring of seabirds oesophageal temperature showed promising results for the detection of prey intake (ANCEL *et al.*, 1997; CHARRASSIN *et al.*, 2001; ROPERT-COUDERT *et al.*, 2000a; 2001a). These loggers are

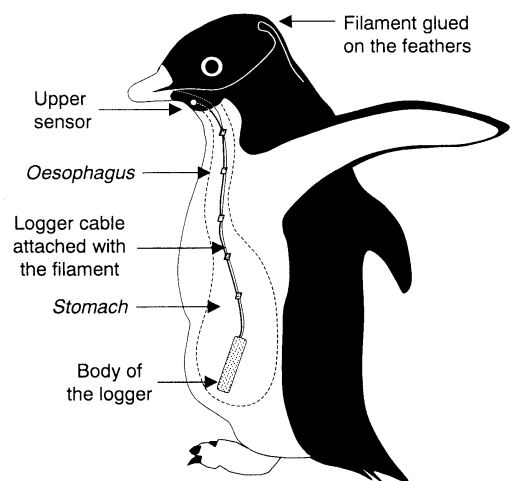


Fig. 2. Presentation and attachment of oesophageal temperature logger (UME-TT generation, Little Leonardo, Tokyo, Japan) illustrated on an Adélie penguin, *Pygoscelis adeliae*. Technicals information about the logger can be found in ROPERT- COUDERT *et al.*, 2000a (see text).

similar to stomach temperature recorders but the thermistors are located in the anterior part of the oesophagus, at the end of a soft plastic cable of various sizes that emerge from the cylindrical body of the logger being placed in the stomach (Fig. 2). Calibration experiments showed that the higher a sensor was placed in the digestive system, the better the detection of prey ingestion (CHARRASSIN *et al.*, 2001) since

prey items are not warmed up and do not cover the sensor. In addition, the time lag between ingestion and the detection of the drop is also considered minimal (ROBERT-COUDERT *et al.*, 2000a). In a study by CHARRASSIN *et al.* (2001) during deployment of oesophageal loggers on free-ranging King penguins, the sensor was kept in position by suturing it to the wall of the oesophagus by surgery that necessitate animal

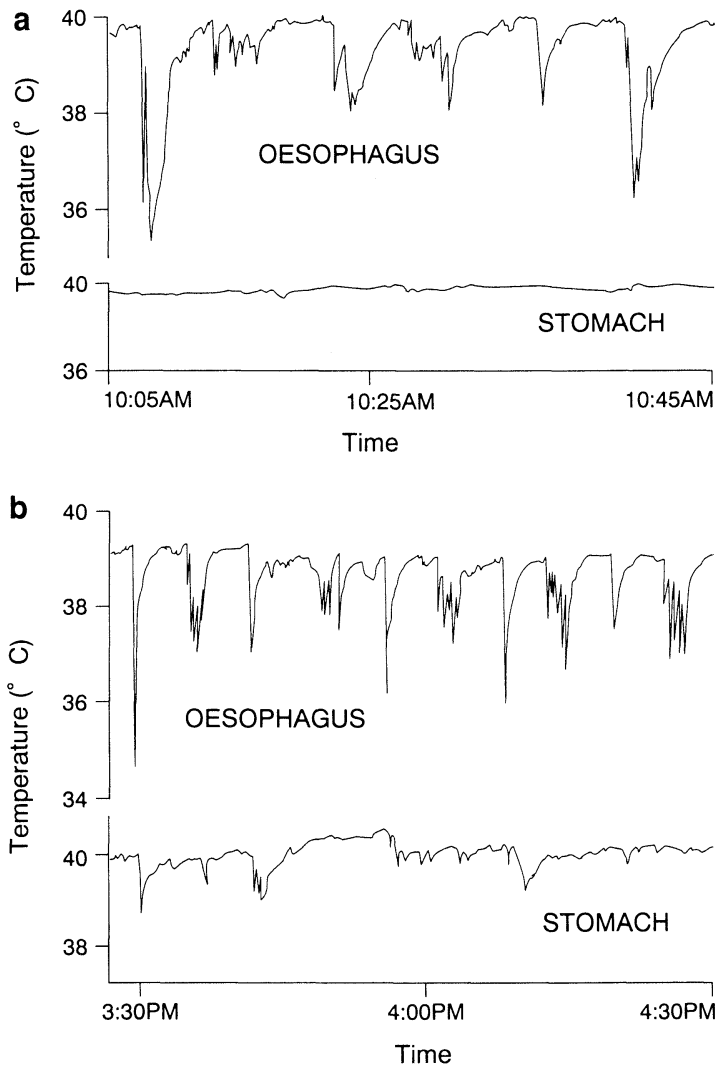


Fig. 3. Internal temperature recordings in the oesophagus and the stomach of captive Adélie penguins, *Pygoscelis adeliae*, with several temperature drops corresponding to the ingestion of Antarctic krills, *Euphausia superba*. In a) the thermistor in the stomach is in direct contact with the stomach wall. In b) both the oesophageal and the stomach thermistors detect prey ingestion but the detection rate in the stomach decreases as the stomach filled. Note in b) the clarity of the temperature drops recorded in the oesophagus compared to that in the stomach.

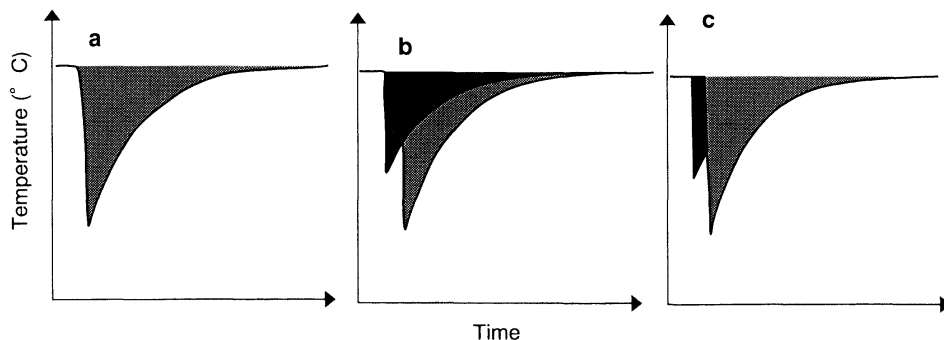
anesthésie. This requires a substantial investment in term of logistics as well as time since a delay is necessary between the operation and the moment the animal can depart to resume normal foraging activity at sea. Therefore, in order to reduce the stress implicit in surgical procedures, a non-invasive method was initially tested on captive Brandts cormorants, *Phalacrocorax penicillatus* Brandt (ANCEL *et al.*, 1997) and successfully applied to free-ranging Adélie penguins (ROBERT-COUDERT *et al.*, 2001 a). Here, the body of the logger was placed in the stomach while the sensor was held suspended in the oesophagus just under the opening of the mouth by a filament externally attached on the plumage of the birds (see Fig. 2). The whole system can be placed on birds in less than 20 minutes and no delay is necessary between fitting and birds release. The main problem encountered with such system is the substantial rejection rate of the logger in the stomach (ROBERT-COUDERT *et al.*, 2001a). However, this can be solved by incorporating a retaining system to the logger such as the anchor system described by WILSON *et al.*, (1998). The reliability of the measurement and the ease of deployment and retrieval of oesophageal temperature devices, as experienced on seabirds, makes it a convenient tool for field studies. However, although the principle is theoretically applicable to any endotherms, oesophageal temperature recording method remains to

be tested on pinnipeds. For such animal, surgery and anesthésie are still a necessity for deploying oesophageal temperature loggers.

4. Progress made due to internal, especially oesophageal, temperature loggers:

Internal temperature loggers have revealed much about the rate of prey ingestion at different scales. Following diel rhythm in vertical migration of prey (WILSON *et al.*, 1993), King Penguins ingest only 17% of the total prey catching during a foraging trip at night (BOST *et al.*, 1997). In being able to ascertain that prey are caught primarily during the day confirmed, in many cases, that seabirds are essentially visual hunters, *e.g.* the Northern Gannet *Sula bassana* (GARTHE *et al.*, 1999). Finally, the identification of the rate of prey ingestion during a specific dive showed that, for instance, both King and Adélie, *Pygoscelis adeliae*, penguins optimize the hunting component of dives by catching a non-negligible percentage of prey during the ascent phase of dives (ROBERT-COUDERT *et al.*, 2000b; 2001a), previously defined as a commuting phase only (see WILSON, 1995 for review).

By using internal temperature logger, it is possible to determine the exact number of prey ingested during a foraging trip and we are now reaching a stage where it will become possible to determine the percentage of prey that is digested at sea. This could help elucidate how



Modified from WILSON *et al.*, 1995

Fig. 4. Schematic diagram showing the problems raised by the calculation of the mass of prey ingested using the integral method when multiple prey are ingested. In a) a single prey is ingested and the calculated integral (shaded area) is a good estimator of the mass of prey ingested. In b) and c) a second prey is swallowed before the asymptote reach the original temperature value and the utilization of the area might underestimate the actual mass of prey ingested. Graphs modified from WILSON *et al.*, 1995 with permission of the author.

birds balance their own body maintenance with the provisioning to their offspring. However, since such investigations depend on the capacity of recording clear temperature drops, oesophageal temperature logger appears to be particularly suitable (Fig. 3, ROBERT-COUDERT *et al.*, 2000a). Internal temperature loggers offer another substantial advantage over other loggers in enabling the mass of food ingested to be more precisely estimated (WILSON *et al.*, 1992). It has been proposed that the energy invested to heat the prey items ingested in the stomach is directly related to the mass of the prey ingested (WILSON *et al.*, 1995). Thus, the mass of prey can be estimated by calculating the integral under the curve of the temperature drop (Fig. 4a; see WILSON *et al.*, 1995 for details), although one should bear in mind that problems occur when several prey are ingested in rapid succession (Fig. 4b; GRÉMILLET and PLÖS, 1994). However, probably due to this confusion effect and in relation with the clearer signal obtained when the sensor is placed closer to the mouth, the magnitude of temperature drop monitored in the oesophagus, has also been shown to be a reliable estimator of the mass of prey swallowed (ROBERT-COUDERT *et al.*, 2000a). Such relationships not only provide information about the mass of prey ingested but can also be used to determine the species ingested. Seabirds, especially penguins, are mainly specialists (CROXALL and LISHMAN, 1987) consuming a limited number of prey species (see review in WILLIAMS, 1995). Within a particular prey species, birds seem even to select a specific category of the prey population, this being well illustrated by Adélie penguins which tend to capture, overall, a greater proportion of gravid females of Antarctic krill *Euphausia superba* (ENDO *et al.*, 2000). The fact that there is often a difference in mass between prey types means that the mass of prey ingested may help identify the prey species captured. By comparing the distribution of diverse prey caught in the three dimensions of a marine ecosystem it may be possible to map overall distribution using marine top-predators. Moreover, the capacity of top-predators to shift from one main target species to secondary ones can be analysed accurately.

In addition, knowledge of the exact amount of prey swallowed provides us with data for calculation of the energy gained by animals at sea. Energetic content of prey can be determined in calorimetric chambers and the corresponding value can be used to quantify the energy gained at sea. Furthermore, using internal temperature loggers, researchers can calculate indices of foraging efficiency, such as the catch per unit effort (abbreviated as CPUE) for marine top-predators (GRÉMILLET, 1997; GARTHE *et al.*, 1999), similar to indices used in fisheries. Such indices consider the percentage of prey caught at a particular depth in relation to the time spent by the predator at that depth and thus, relies on an accurate determination of all prey ingested. An example of a CPUE calculated on a free ranging Adélie penguin is shown in Fig. 5. In this figure the depth zones of maximum hunting success are easily visualized. Moreover, the amount of energy gained per unit of time at sea can be determined and examined with regards to the amount of energy required expended by the birds and the amount of energy by the offspring. This is relevant in the context of analysis of energy balances and of the breeding success of animals that are exploiting a fluctuating environment.

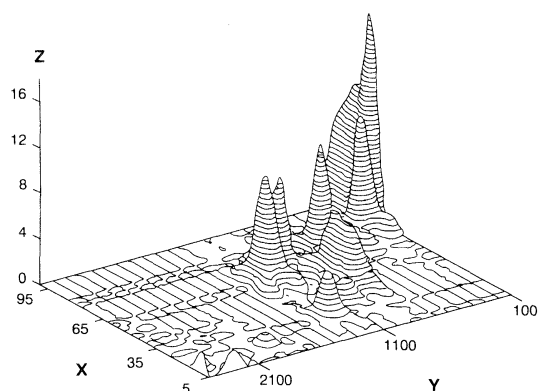


Fig. 5. Catch per unit effort (CPUE, see text) in a free-ranging Adélie penguin, *Pygoscelis adeliae*, equipped with oesophageal temperature logger in tandem with a depth logger. X, Y and Z axis are the maximum diving depth (m), the time spent per depth unit (s) and the CPUE value, respectively.

The previous paragraphs showed the potential in internal temperature loggers for the detection of the timing of prey intake or amount of food ingested. Such information can be used to estimate energy gained per individual and /or to quantify marine resources. However, determination of the exact moment a prey is swallowed also allows researchers to unravel the foraging strategies that lead to successful prey capture. Indeed, thanks to the timing of capture, it is possible to distinguish successful from unsuccessful dives and to compare their characteristics. To perform this type of analysis, one should be able to record multiple data per individual, including the internal temperature as direct indication of feeding. Although the technologies permitting large amount of data to be stored in loggers are relatively recent, some studies have clearly demonstrated the benefits derived from this integrative approach. Thus, the simultaneous recording of depth utilization, swim speed and oesophageal temperature of free-ranging Adélie penguins has demonstrated how these birds change their dive angle and swim speed according to prey encounter (ROPERT-COUDERT *et al.*, 2001a; 2001b). Apart from confirming or refuting previous hypotheses about the marine top-predators foraging strategies based on simple observation of depth or speed profiles (cf. beginning of paragraph 3), the use of accurate, direct recording of the feeding activity of marine animals in tandem with the monitoring of other parameters, has meant that a whole new area of science is opened to investigation.

5. Conclusions-Perspectives

Regarding the results presented in this review, direct measurement of the feeding activity is not only a parameter in itself, it is also a basis from which various parameters and information derive, offering several levels of analysis. To be complete, one should mention that further progress in the described methodology is still needed. Internal temperature drops can have various origins. For example, it remains difficult in some instances to differentiate between the ingestion of prey and the ingestion of water or ice: this has been shown to occur in seals (GALES and RENOUF, 1993) as well as in

Adélie penguins (ROPERT-COUDERT *et al.*, 2001a). Multiple data recording could thus be critical in helping address this problem. In addition, the effect of logger attachment has been carefully investigated and loggers have been constantly improved in order to reduce the stress incurred by the animals. However, development of less invasive methods is still regarded as important. In addition, ameliorations should be added to present methods so that their application can extend to various species of marine predators with different feeding and foraging habits.

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Allozyme determination of genetic diversity in Japanese and Thai populations of Oval Squid (*Sepioteuthis lessoniana* Lesson, 1830)

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Abstract : Genetic variation and genotypic population structure of two geographic populations of oval squid (*Sepioteuthis lessoniana* Lesson, 1830), captured from Nagasaki (Japan) and Rayong (Thailand) were investigated using multi-locus allozyme analysis. On the basis of 22 loci screened, the percentage of polymorphic loci and observed heterozygosity were 45.45 % and 0.28 for Japanese and 50.00 % and 0.23 for Thai populations, respectively. These results suggest relatively high genetic diversity within the representative populations of *S. lessoniana*. At the same time, low genetic distances between these population were observed ($D=0.003$). A lack of genetic differentiation between the Japanese and Thai populations of *S. lessoniana* suggests a panmictic gene pool of *S. lessoniana* over a wide geographic area.

Key words : Thailand, population genetics, squid, *Sepioteuthis*, electrophoresis

1. Introduction

At least 31 cephalopod species belonging to 17 genera and 10 families are recognized in Thai waters (CHOTIYAPUTTA, 1993). The annual catch of cephalopods in Thailand accounts for 5.6 % of the total catch of all marine organisms (Department of Fisheries, 2000). Among the described species, the oval squid (*Sepioteuthis lessoniana*) is one of the most landed. This species also has potential to be cultured commercially (LEE *et al.*, 2001) and is therefore, regarded as one of the most important cephalopod species in Thailand (NABHITABHATA, 1978 and 1985).

Generally, *S. lessoniana* can be found from the sea surface down to approximately 100m in depth (ROPER, *et al.*, 1984). It is distributed over a wide geographic area covering most of the

Indo-Pacific region, the Indian ocean, Thailand, Indonesia, northern Australia, north-to-central Japan and eastward of the Hawaiian Islands (CARPENTER and NIEM, 1998).

Knowledge on genetic variation levels and population differentiation of *S. lessoniana* is important for the design and implementation of appropriate fisheries management programs. However, relatively little is known about the intraspecific genetic variability of this squid in Thailand. This information is crucial to a rational decision whether the exploited species need to be conserved or further exploited (CAVALHO and HAUSER, 1994).

Accordingly, gene flow is one of the most important factors responsible for intraspecific differentiation of organisms (AVISE, 1994). WARD and GREWE (1994) compared results from population genetic studies of more than 300 animal species and concluded that mobility is the most important factor reflecting the apparent magnitude of intraspecific subdivisions. Therefore, it is not surprising that vagile organisms (high degree of gene flow) have lower levels of population differentiation than do relatively sedentary species. The appropriate genetic markers can be utilized to assist taxonomic iden-

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tification and to increase fisheries management efficiency in various taxa (KLINBUNGA *et al.*, 2000). In cephalopods, allozyme analysis has been used for population genetic and systematic studies in several loliginid squids (ALLY and KECK, 1978; CHRISTOFFERSON *et al.*, 1978; SMITH *et al.*, 1981; GARTHWAITE *et al.*, 1986; NATSUKARI *et al.*, 1986; AUGUSTYN and GRANT, 1988; CARVALHO and LONEY, 1989).

Population genetic studies in Thai squids are quite limited compared to literature available from other regions of the Western Pacific (IZUKA *et al.*, 1994, 1996; YOKOGAWA and UETA, 2000). Furthermore, there have been few publications documenting genetic diversity of *S. lessoniana* from Thai populations (see IZUKA *et al.* 1996). The objectives of this study were twofold. The first objective was to examine the level of genetic diversity of *S. lessoniana* captured from a major Thai fishing ground. The second objective, was to determine whether intraspecific population subdivision exists in representative geographic samples, by allozyme analysis of *S. lessoniana* collected from Japan and Thailand.

2. Materials and Methods

Sampling

Ninety individuals of the oval squid (*S. lessoniana*) originating from Rayong ($N=50$) located in the Gulf of Thailand and Nagasaki, Japan ($N=40$) were captured. Specimens from Thailand were kept at -70°C and transported to Nagasaki University on dry ice. Oval squid from Nagasaki were captured locally and kept -80°C . At the Laboratory of Fisheries Biology, Faculty of Fisheries, Nagasaki University, liver tissue, mantle and buccal mass were dissected out from each squid from both populations and subjected to allozyme analysis.

Allozyme Analysis

Frozen tissue samples were homogenized mechanically in 0.25 ml of deionized water. Total solute proteins extracted from each individual were electrophoretically analyzed utilizing horizontal starch gel (11%) with 3 different buffer systems namely, C-A (pH 7.0), CAME (pH 6.8) and TC (pH 8.0) (SHAW and PRASAD, 1970; AEBERSOLD *et al.*, 1972; CLAYTON and

TRETIK, 1972). The starch gels were subsequently stained with 12 enzymes (Table 1).

Data Analysis

Banding patterns on the gels were interpreted as reflecting inherited Mendelian genetics predicted by the subunit composition of each enzyme (MAY, 1992). Observed and expected heterozygosity were calculated (NEI, 1987). The average effective number of alleles was examined according to CROW and KIMURA, (1965). Allele frequencies at each locus of each geographic samples were calculated and analyzed against Hardy-Weinberg equilibrium using goodness-of-fit (G) statistics. Genetic similarity and divergence were estimated using Roger's similarity index (R) (ROGER 1972) and Nei's genetic identity (I) and distance (D) (NEI, 1987), respectively. Geographic heterogeneity in allele distribution frequencies between populations was also analyzed using the G statistic.

3. Results

Twelve enzymes were successfully resolved and used for analysis of allozyme polymorphism in Thai and Japanese *S. lessoniana*. These accounted for a total of 22 putative loci (Table 1). A fixed allele was observed in 50% of screened loci ($AK-3^*$, $AK-4^*$, $AK-5^*$, ACP^* , $DIA-6^*$, $DIA-3^*$, $G3PDH-1^*$, $G3PDH-2^*$, $IDHP-1^*$, $IDHP-2^*$ and $MDH-1^*$). Eleven loci (MDH^* , $PGDH^*$, $DIA-1^*$, ATT^* , $AK-1^*$, $AK-2^*$, ALP^* , MPI^* , GPI^* , $PGM-1^*$ and $PGM-2^*$) were indicated. Polymorphism was estimated at 5% with the most common allele being less than 95% overall in investigated specimens. Seven, six and five polymorphic allozymes could be detected in the buccal mass, muscle and liver tissue, respectively.

Good agreement between observed and expected heterozygosity of each *S. lessoniana* population suggested Hardy-Weinberg equilibrium in each population of *S. lessoniana* at all loci. All the examples were regarded as representing simple Mendelian populations. However, fixed alleles that can differentiate Thai and Japanese *S. lessoniana* populations were not observed. Generally, similar levels of allele frequencies were observed across all loci

Table 1. The numbers of alleles, protein structure, electrophoretic buffer systems, and tissue sources of allozymes screened in this study.

Enzyme	Abbreviation	Tissue	Buffer System	No of Alleles	Protein Structure	D
Glycerol-3-phosphate dehydrogenase	<i>G3PDH-1*</i>	M	3	1	Tetramer	>0.95
	<i>G3PDH-2*</i>	M	3	1		
Malate dehydrogenase	<i>MDH-1*</i>	M	1	1	Dimer	
	<i>MDH-2*</i>	M	1	2	Dimer	>0.95
Isocitrate dehydrogenase	<i>IDHP-1*</i>	M	1	1	Dimer	>0.95
	<i>IDHP-2*</i>	M	1	1		
Phosphogluconate dehydrogenase	<i>PGDH*</i>	B, L	1	3	Dimer	<0.95
Diaphorase	<i>DIA-1*</i>	B, L	2	2	Monomer	<0.95
	<i>DIA-2*</i>	B, L	2	1	Monomer	
	<i>DIA-3*</i>	B, L	2	1	Monomer	
Aspartate aminotransferase	<i>AAT*</i>	B, L	1	2	Dimer	<0.95
Adenylate kinase	<i>AK-1*</i>	M	1	2	Monomer	<0.95
	<i>AK-2*</i>	M	1	2	Monomer	<0.95
	<i>AK-3*</i>	M	1	1	Monomer	>0.95
	<i>AK-4*</i>	M	1	1	Monomer	>0.95
	<i>AK-5*</i>	M	1	1	Monomer	>0.95
Alkaline phosphate	<i>ALP*</i>	B, L	2	2	Monomer	<0.95
Acid phosphatase	<i>ACP*</i>	M	3	1	Dimer	>0.95
Mannose phosphate isomerase	<i>MPI*</i>	M	3	2	Monomer	<0.95
Glucose phosphate isomerase	<i>GPI*</i>	B, L	1	3	Dimer	<0.95
Phosphoglucomutase	<i>PGM-1*</i>	M, B	1	2	Monomer	<0.95
	<i>PGM-2*</i>	M, B	1	2	Monomer	<0.95

Buffer system: 1=C-A pH 7.0, 2=CAME pH 6.8, 3=TC pH 8.0;

Tissues: M=mantle, B=buccal mass, l=liver

P=frequency of common allele for polymorphic locus.

except those of *GPI** and *MDH-2**, which showed significant differences between localities ($P < 0.05$). The Thai squids showed low frequency of alleles a (0.11) and b (0.13) of each respective locus of *MDH-2** and *GPI** but these alleles were not detected in the Japanese *S. lessoniana* population (Table 2).

The average effective number of alleles per locus in *S. lessoniana* was 1.09. The percentage of polymorphic loci at 5% level and an average heterozygosity of the Japanese *S. lessoniana* were 45.45% and 0.28, whereas those of the Thai population was 50.00% and 0.23, respectively (Table 2). Both Nei's genetic identity ($I = 0.997$) and Roger's similarity index ($R = 0.973$) were comparable. The genetic distance ($D =$

$-\ln I$) was 0.003 suggesting close genetic relationship between these populations. Geographic heterogeneity analysis did not indicate any difference in allele distribution frequency between the Japanese and Thai *S. lessoniana* for all loci ($P > 0.05$).

Discussion

Population differentiation within a particular species is influenced by several factors such as, migration (or gene flow), random genetic drift, modes of natural selection, mutation and genetic recombination through mating systems. Additionally, biological factors related to individual groups of organisms for instance, ecological factors and life history (SEGAWA *et*

Tabel 2. Allele frequencies, percentage of polymorphic loci, effective number of alleles and observed heterozygosity of two conspecific populations of *S. lessoniana* originating from Japan and Thailand based on allozyme analysis.

Locus	Allele	Geographic population	
		Japan (Nagasaki) (N=39-40)	Thai (Rayong) (N=25-50)
AAT*	*a	0.885	0.837
	*b	0.115	0.163
AK-1*	*a	0.461	0.227
	*b	0.538	0.773
AK-2*	*a	0.526	0.660
	*b	0.474	0.340
ALP*	*a	0.125	0.390
	*b	0.875	0.610
DIA-1*	*a	0.387	0.357
	*b	0.612	0.643
GPI*	*a	0.525	0.859
	*b	0	0.128
	*c	0.475	0.013
MDH-2*	*a	0	0.110
	*b	1	0.890
MPI*	*a	0.500	0.437
	*b	0.500	0.562
PGDH*	*a	0.075	0.033
	*b	0.862	0.7935
	*c	0.062	0.174
PGM-1*	*a	0.475	0.462
	*b	0.525	0.537
PGM-2*	*a	0.175	0.150
	*b	0.825	0.850
% Polymorphic loci		45.45	50.00
Effective number of alleles		1.09	1.09
Expected heterozygosity (Hobs)		0.179	0.183

N=number of individuals assayed.

al., 1993), also play a partitioning role in population differentiation (RYMAN and UTTER, 1987; AVISE, 1994).

There have been no publications estimating genetic variation levels in *S. lessoniana* in Thailand specifically. Whereas, some Japanese populations have been found to be quite variable genetically (IZUKA *et al.*, 1994; YOKOGAWA and UETA, 2000). Although the sample sizes used in this study were small, specimens were collected from two sampling sites located over

thousands of kilometers in distance. Our preliminary results should be reliable for determination of genetic differentiation within this species at macrogeographic scales. Nevertheless, larger numbers of populations should be collected before an unambiguous conclusion on intraspecific genetic differentiation can be drawn in *S. lessoniana* from populations in closer geographical proximity.

Information from Japanese fishermen reveals that there are groups of this species (AKAIKA, SHIROIKA and KUAIKA) distinguished by body color, shape and meat quality. Such differences in appearance have not been reported in Thailand. Allozyme studies on these groups suggest genetic differences at the subspecific rather than intraspecific level of a single species (IZUKA *et al.*, 1994). According to IZUKA *et al.* (1996), *S. lessoniana* (SHIROIKA) from Honshu, Shikoku, Ryukyu Islands and Thailand share a common gene pool over their 2,000 km geographical distance. This SHIROIKA group is a widely distributed subspecies in the tropical to warm temperate areas of the northwestern Pacific (IZUKA *et al.*, 1994). Although comparative morphology studies were not carried out, it may be possible that the SHIROIKA group is closely related to populations of *S. lessoniana* in Thailand. This is reflected in lack of genetic differentiation between this Japanese and Thai *S. lessoniana* revealed by allozyme polymorphism. These conclusions suggest that *S. lessoniana* may share a panmictic gene pool over a wide geographic area. Such patterns may have been mediated by a shared geological history governed by oceanic currents. The high % polymorphic loci and heterozygosity of *S. lessoniana* in this study reflects a large effective population size. Thus, localized genetic adaptation may take place with very little differentiation at neutral loci. The absence of obvious physical barriers between these two regions might have resulted in a high gene flow level of this species. Considering external morphology of *S. lessoniana*, the large conspicuous fin implies that it is a vagile species (ROPER *et al.*, 1984). Therefore, the Thai and some Japanese gene pools may have become homogenised by its migratory ability. Conformation of Hardy-Weinberg equilibrium

as revealed by non-significant difference between observed and expected heterozygosity of *S. lessoniana*, indicates that specimens used in this study were sampled from a large random mating population. However, a comparatively greater genetic differentiation of this squid between other locations in closer proximity (IZUKA *et al.*, 1996) could be due to smaller effective population sizes, local adaptation, less potential of gene flow and time of separation. Some groups of the species within Japanese waters seem to have barriers to panmixia. Most notables are oval squid populations surrounding the Ogasawara Islands and other sampling localities. Is it possible that the Kuroshio Current can act as a natural barrier to migration? The oval squid populations in Japan have distinct differences in genetic distance values (YOKOGAWA and UETA, 2000). The squid populations in Japanese localities are probably under heavy fishing pressure. This is suggested by the relatively low average percentage of polymorphic allozyme loci and heterozygosity values.

The percentage of polymorphic allozyme loci in *S. lessoniana* in this study from both Royong and Nagasaki was quite high and comparable to that previously reported in the squids, *L. chinensis* (45.5–54.45%), *Ommastrephes batramii* (46%) and *Beryteuthis magister* (43%) (KATUGIN, 1993; YEATMAN and BENZIE, 1993). However, our reported values were much higher than that of other groups of *S. lessoniana* within the southwestern Japan complex (19.3%) (IZUKA *et al.*, 1996). Low percentage of polymorphic loci has also been reported for other *Loligo* species with values ranging from 0 to 29% (GARTHWAITE *et al.*, 1986; AUGUSTYN and GRANT, 1988; CARVALHO and LONEY, 1989; YEATMAN and BENZIE, 1993).

Apart from polymorphic loci, average heterozygosity of *S. lessoniana* reported in this study is also higher than that of the same species in southwestern Japan ($H=0.037$) (IZUKA *et al.*, 1996) and other loliginid species. Some examples are heterozygosity values reported for *L. plei* ($H=0$), *L. brevis* ($H=0$) and *L. pealei* ($H=0.006$), (GARTHWAITE *et al.*, 1986), *L. opalescence* ($H=0.037$) (AUGUSTYN and GRANT, 1988), *L. vulgaris reynandii* ($H=0.030$) and *L. gahi*

($H=0.059$) (CARVALHO and LONEY, 1989), *L. bleekeri* ($H=0.003$) (SUZUKI *et al.*, 1993), and *L. chinensis* ($H=0.006\sim 0.009$) (YEATMAN and BENZIE, 1993).

The difference in genetic diversity in *S. lessoniana* detected by allozyme analysis reflects the potential of this simple approach for population genetic studies. Results may be applied to fisheries management regime of *S. lessoniana* at least on a macrogeographic scale. Therefore, more extensive surveys of genetic diversity and differentiation of this squid should be further carried out over other areas of its distribution. More emphasis could be placed on populations in closer proximity in Thailand. Additional molecular approaches, for example; random amplified polymorphic DNA (RAPD), restriction analysis of PCR-amplified mtDNA genes and single copy nuclear DNA polymorphism (scnDNA) can also be utilized to ensure more precise conclusions on oval squid stock structure.

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Seasonal variation of the oceanic condition along the southern coastal area of Java to Sumbawa, Indonesia

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Abstract : Field observations to understand seasonal variability of the oceanic condition along the southern coastal area of Java to Sumbawa were conducted in the northwest monsoon (April-May 1990) and the southeast monsoon (August-September 1990). The observation was focused on the monitoring of physical (potential temperature, salinity, $\sigma\text{-}\theta$), chemical (phosphate, nitrate, silicate), and biological (chlorophyll-*a*, DO) characteristics through the season. The oceanic condition was found to be mainly affected by seasonal change of precipitation and upwelling related to the monsoon. The upwelling occurrence in the eastern part of this region was clearly seen by increasing nutrients concentration, especially nitrate and decreasing water temperature at the surface due to the southeast monsoon. The nitrate was a limiting factor for photosynthesis within this region.

Key words : Seasonal variation, oceanic condition, southern coastal area of Java to Sumbawa

1. Introduction

The southern coastal area of Java to Sumbawa is well known as one of the most productive area of the oceanic migratory fish such as skipjack and tuna in the western Indonesia due to upwelling. That situation has attracted some investigators to observe the upwelling phenomena in and around this area from various points of view. WYRTKI (1962) demonstrated the upwelling occurrence within this region by ascending of low water temperature and rich nutrient (phosphate) water mass near thermocline (200 m) to the surface in the southern part of Sumbawa during the southeast monsoon. PURBA(1995) found the upwelling by SST(Sea Surface Temperature) distribution in the narrow areas of the western Java.

Detailed information of the oceanic condition, however, is still very limited, particularly from the view point of conventional parameters and nutrients distribution as well as their

variability in the different seasons along the southern coastal area of Java to Sumbawa. Since the area is considered to be affected by the monsoon (TOMASCIK *et al.*, 1997), seasonal observation of the oceanic condition is necessary to be conducted within this region in order to confirm the upwelling situation related to the monsoon. The seasonal change is suspected to have strong effect on the water characteristic variability and their distribution in the water column.

To understand seasonal variability of the oceanic condition along the southern coastal area of Java to Sumbawa, we observe the distribution of water temperature, salinity, phosphate, nitrate, silicate, dissolved oxygen and chlorophyll-*a* during the northwest and southeast monsoons.

2. Observations

Intensive observations using R. V. Barunajaya I of The Agency for the Assessment and Application of Technology (BPPT) were carried out to collect the numerous data of physical (water temperature and salinity), chemical (phosphate, nitrate and silicate) and biological (chlorophyll-*a* and dissolved oxygen) parameters. These observations were conducted in

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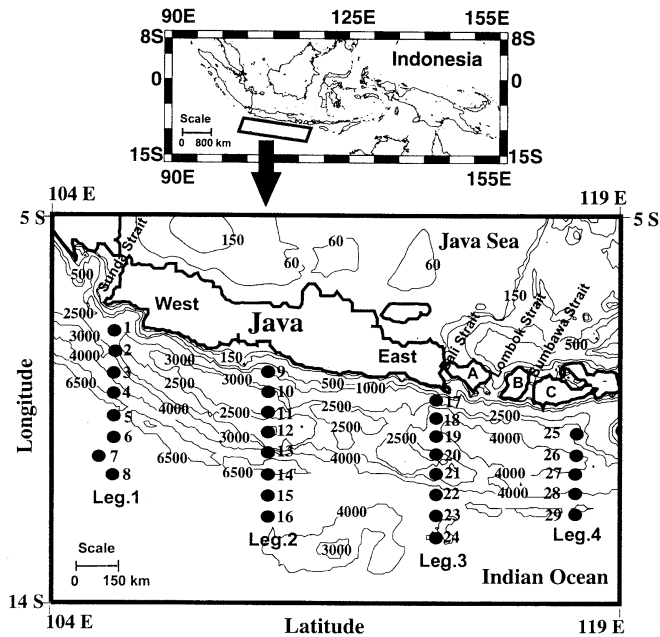


Fig. 1. Study area, observation stations (●) and bathymetry (m) along the southern coastal area of Java to Sumbawa. A denotes Bali Island, B and C are Lombok and Sumbawa Island, respectively. Western part is represented by Legs. 1 and 2, and eastern part by Legs. 3 and 4.

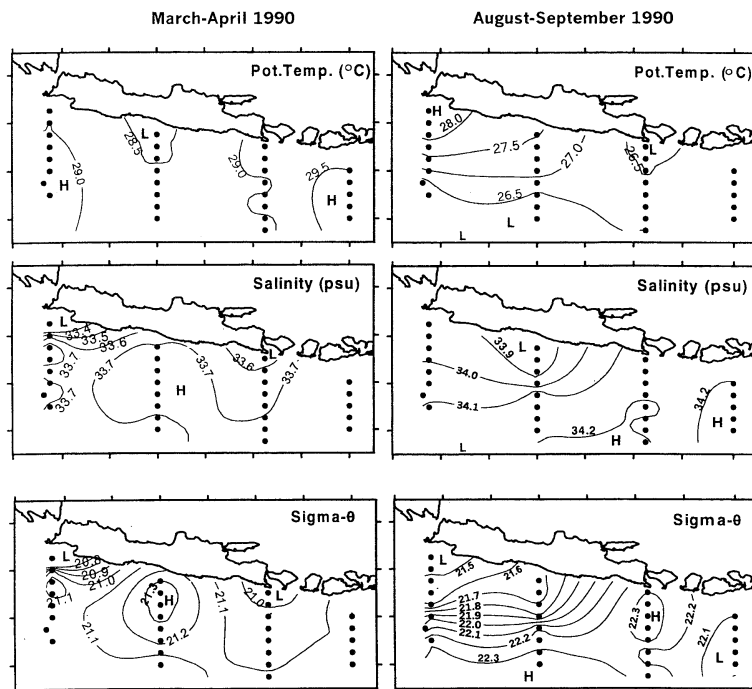


Fig. 2(a). Horizontal distributions of potential water temperature (°C), salinity (psu) and sigma- θ at the surface layer

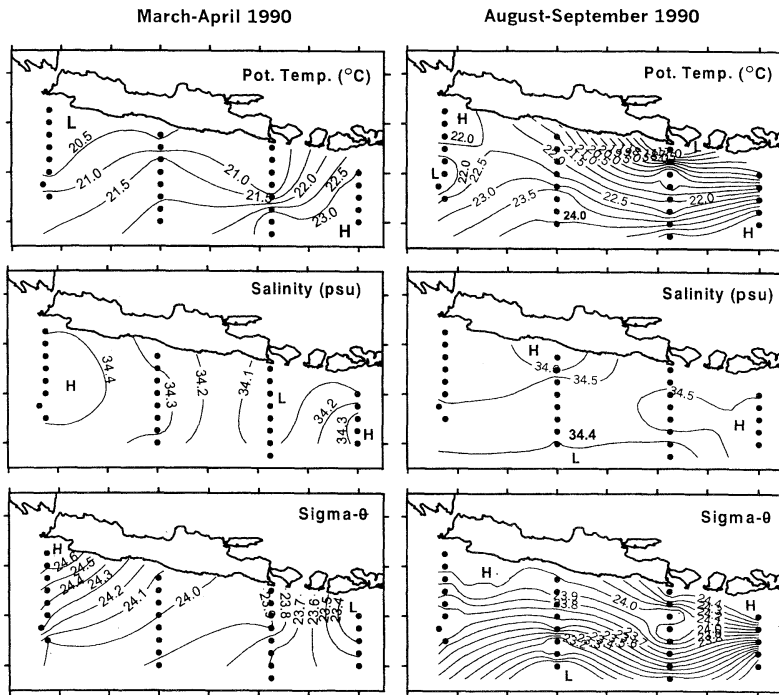


Fig. 2(b). Horizontal distributions of potential water temperature (°C), salinity (psu) and sigma-θ at 100m depth.

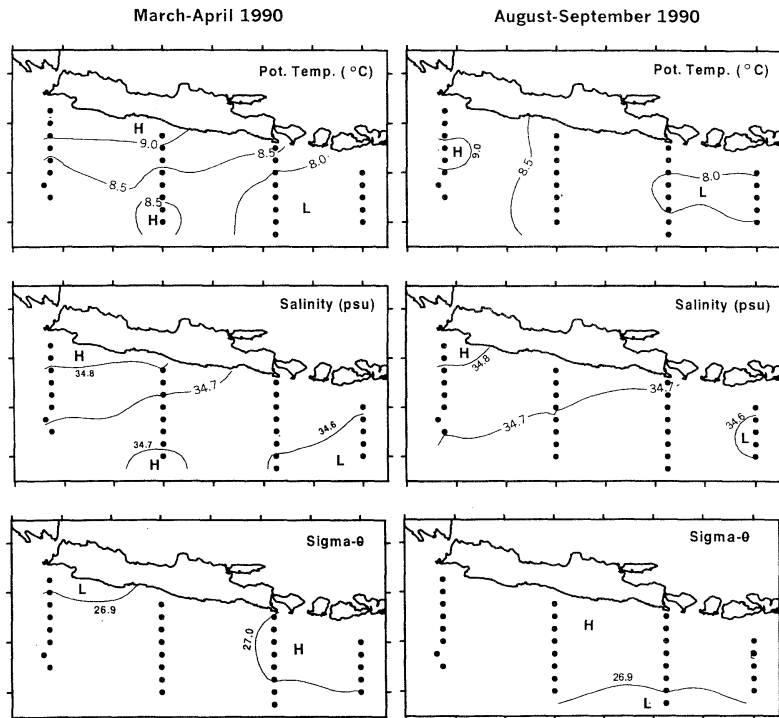


Fig. 2(c). Horizontal distributions of potential water temperature (°C), salinity (psu) and sigma-θ at 500m depth.

March–April 1990 (northwest monsoon) and August–September 1990 (southeast monsoon) at 29 stations along the southern coastal area of Java to Sumbawa. The observation stations are divided into four parallel Legs from the western (Leg. 1 and 2) to the eastern part (Leg. 3 and 4). The distance between Legs is 500 km and that between stations of each Leg is 50 km. The station number of Leg. 1 to Leg. 3 is 8 stations, and that of Leg. 4 is 5 stations (Fig. 1).

To understand vertical distributions of physical parameters, CTD of the Guildline type was deployed up to 600 m depth to record a series of water temperature and salinity. Potential water temperature and σ_t was then calculated from water temperature, salinity and the depth (UNESCO, 1973). A series of chemical and biological data (phosphate, nitrate, silicate and dissolved oxygen) were obtained by analyzing water samples at various depths, which were withdrawn from 12 Niskin bottles attached to CTD. Phosphate, silicate and nitrate were then measured by Technicon Auto Analyzer and dissolved oxygen by Winkler method (U.S. Hydrographic Office, 1959). Biological parameter (chlorophyll-*a*) was obtained by filtering water samples at various depth using 0.45μ Millipore filter HA WP with diameter of 47 mm and was then extracted by 90% acetone and measured by spectrophotometer with the wave length of 665, 645 and 630 nm (STRICKLAND and PARSON, 1968). HELLERMAN and ROSENSTEIN (1983) monthly mean wind stress data derived from 1870–1976 for April, May, August and September with resolution of $2^\circ \times 2^\circ$, and bathymetry data of the National Geophysical Data Center (NGDC) with resolution of $5' \times 5'$ were also collected to support this study.

3. Results

3.1. Potential water temperature, salinity and σ_t

Horizontal distributions of potential water temperature, salinity and σ_t at the surface layer, 100 m and 500 m depths are shown in Figs. 2 (a), (b), and (c), respectively. In the northwest monsoon, potential water temperature is 28.5–29.5 °C at the surface layer, 20.5–23.0 °C at 100 m depth and 8.0–9.0 °C at 500 m

depth. In the southeast monsoon, potential water temperature is 26.5–28.0 °C at the surface layer, 16.0–25.0 °C at 100 m depth and 8.0–9.0 °C at 500 m depth.

In the southeast monsoon, potential water temperature at the surface and 100 m depth are lower than that in the northwest monsoon. Moreover, during the southeast monsoon, potential water temperature at the surface layer of the eastern part (Leg. 3) is remarkably lower than that in the western part (Leg. 1). The similar situation is also found at 100 m depth. The lowest potential water temperature of those layers mainly appears in the nearshore of the southern coastal area of east Java to Bali (Stas. 17 and 18 of Leg. 3) and it spread southwestward to the offshore. At 500 m depth, potential water temperature is stable with the similar pattern in both seasons, that is, high in the western part (Leg. 1) and low in the eastern part (Leg. 3).

In the northwest monsoon, salinity and σ_t at the surface layer are within 33.3–33.7 psu and 20.7–21.3, respectively, those at 100 m depth are 34.1–34.4 psu and 23.4–24.6 and those at 500 m depth are 34.6–34.8 psu and 26.9–27.0. In the southeast monsoon, salinity at the surface layer, 100 m depth and 500 m depth are within 33.9–34.2 psu, 34.4–34.6 psu and 34.6–34.8 psu, respectively. σ_t is within 21.5–22.3 at the surface layer, 23.0–24.4 at 100 m depth and 26.9–27.0 at 500 m depth. Salinity and σ_t at the surface layer in the northwest monsoon are lower than those in the southeast monsoon. At 100 m depth, salinity is also lower, but σ_t is higher in the northwest monsoon. At 500 m depth, salinity and σ_t in both seasons are almost stable in the similar range. In addition, salinity and σ_t at the surface layer both seasons show almost the similar pattern, that is, low in the western part (Leg. 1) and high in the eastern part (Leg. 3) and on the contrary at 100 m depth. The different situation, however, is seen at 500 m depth where salinity in both seasons is high in the western part (Leg. 1) and low in the eastern part (Leg. 3).

Vertical distributions of potential water temperature, salinity and σ_t along Leg. 1 and Leg. 3 are shown in Figs. 3(a) and (b),

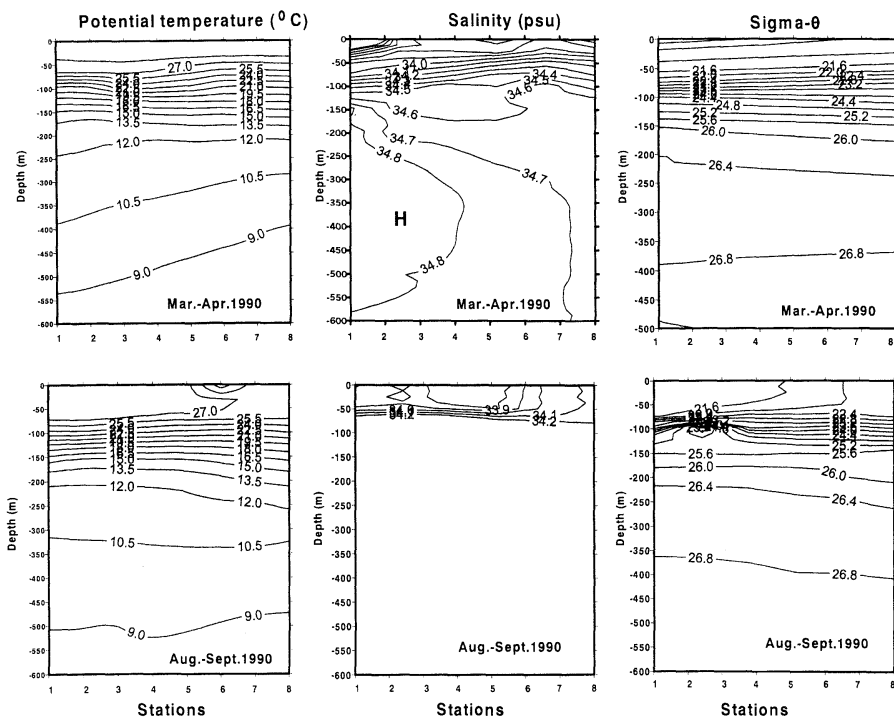


Fig. 3(a). Vertical distributions of potential water temperature ($^{\circ}\text{C}$), salinity (psu) and sigma- θ along Leg. 1.

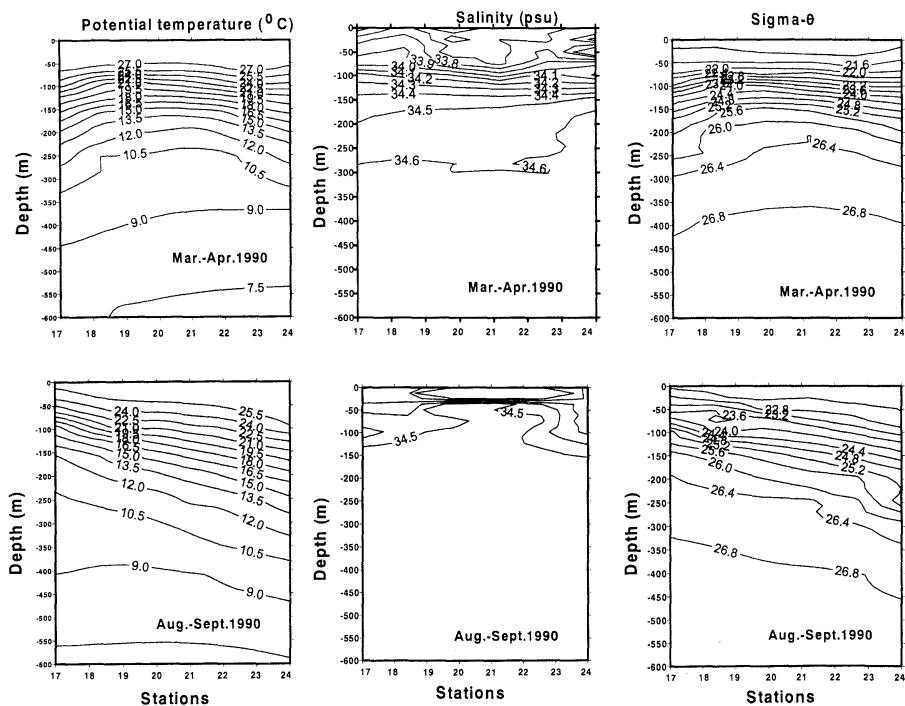


Fig. 3(b). Vertical distributions of potential water temperature ($^{\circ}\text{C}$), salinity (psu) and sigma- θ along Leg. 3.

respectively. Vertical distributions of potential water temperature along Leg. 1 (western part) and Leg. 3 (eastern part) show almost the similar pattern and well stratified in both seasons. In the surface layer, however, potential water temperature during the northwest monsoon (March–April) in the western part (Leg. 1) is slightly lower than that in the eastern part (Leg. 3) and the contrary situation is found in the southeast monsoon (August–September). The lowest water temperature less than 25.5 °C in the southeast monsoon is found near the shore of southern coast of east Java (Sta. 17 and 18) in the eastern part (Leg. 3) with shoreward ascending of the isotherm. The reversal situation with the off-shoreward ascending of potential water temperature is found in the northwest monsoon, especially at the depth below 250m in both western (Leg. 1) and eastern parts (Leg. 3). The similar ascending pattern is also found in sigma- θ distribution. Moreover, sigma- θ at the surface layer in the western part (Leg. 1) is slightly lower than that in the eastern part (Leg. 3) in the northwest monsoon and contrary in the southeast monsoon. Different situation is seen in salinity distribution. It is well stratified in the northwest monsoon and vertically well mixed in the southeast monsoon. High salinity water more than 34.8 psu intrudes in the western part (Leg. 1) at the depth below 200m from the near shore region during the northwest monsoon.

3.2. Nutrients and DO

Horizontal distributions of nutrients (phosphate, nitrate and silicate) and DO at the surface layer, 100m and 500m depths during the northwest and southeast monsoons are shown in Fig. 4(a), (b) and (c), respectively. Phosphate concentration at the surface layer does not show a significant difference between the northwest and the southeast monsoon and they are within 0.12–0.27 μ mol/l. The similar situation is also found on the silicate concentration, and they are within 5–9 μ mol/l. Higher concentration of phosphate and silicate in both seasons are found at the near shore region of southern part of the central Java to Sumbawa. On the other hand, nitrate concentration shows a significant difference between the seasons

and it is higher in the southeast monsoon, almost 2 to 5 times than that in the northwest monsoon. Nitrate concentration in the southeast monsoon is within 0.5–2.3 μ mol/l, but that in the northwest monsoon is within 0.3–0.5 μ mol/l. The highest concentration of nitrate is also found at the same area with phosphate and silicate.

At 100m depth, phosphate concentration in the southeast monsoon is slightly higher than that in the northwest monsoon. Phosphate concentration in the southeast and northwest monsoons is 0.72–1.62 μ mol/l and 0.72–1.12 μ mol/l, respectively. The similar situation is seen on silicate concentration, that is within 9–11 μ mol/l for both seasons. Nitrate concentration shows significant difference between the seasons, that in the southeast monsoon is higher than that in the northwest monsoon. Nitrate concentration in the southeast monsoon is within 3.7–19.1 μ mol/l and that in the northwest monsoon within 3.7–10.3 μ mol/l. For these nutrients, the highest concentration is seen in the near shore region of southern coastal area of Java to Sumbawa.

At 500 m depth, phosphate and nitrate in the southeast monsoon is slightly lower and higher than those in the northwest monsoon, respectively. Phosphate concentration is within 1.97–2.27 μ mol/l in the northwest monsoon and 1.97–2.17 μ mol/l in the southeast monsoon. Nitrate concentration is within 24.7–33.5 μ mol/l in the northwest monsoon and 29.1–33.5 μ mol/l in the southeast monsoon. Silicate concentration is within 51–65 μ mol/l for both seasons. As similar as at the surface and 100 m depth, the highest concentration of phosphate, nitrate and silicate at 500m depth is also found around the near shore region of southern coastal area of Java to Sumbawa.

Meanwhile DO concentration at the surface layer shows slight difference between the seasons. The DO concentration in the southeast monsoon and northwest monsoon is within 3.95–4.45 ml/l and 4.35–4.45 ml/l, respectively. DO concentration is slightly lower in the southeast monsoon than that in the northwest monsoon. Higher concentration of DO in the southeast monsoon is seen at the southern part of east Java to Sumbawa and that in the northwest

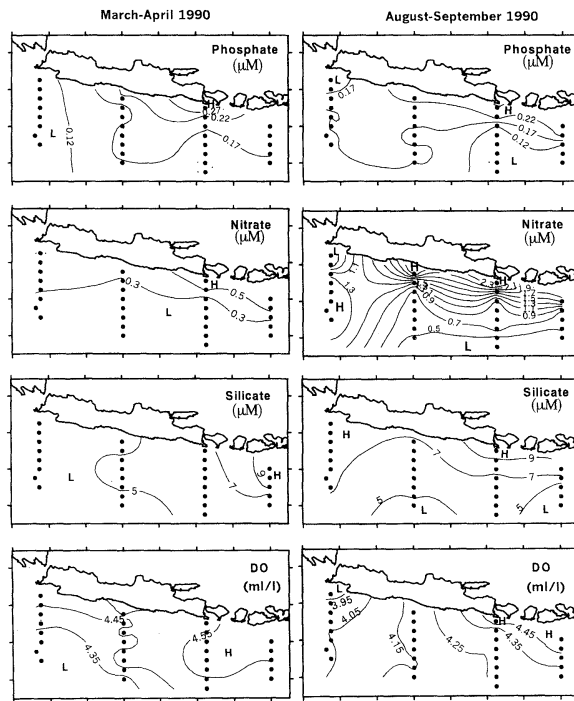


Fig. 4(a). Horizontal distributions of phosphate ($\mu\text{ mol/l}$), nitrate ($\mu\text{ mol/l}$), silicate ($\mu\text{ mol/l}$) and DO (ml/l) at the surface layer.

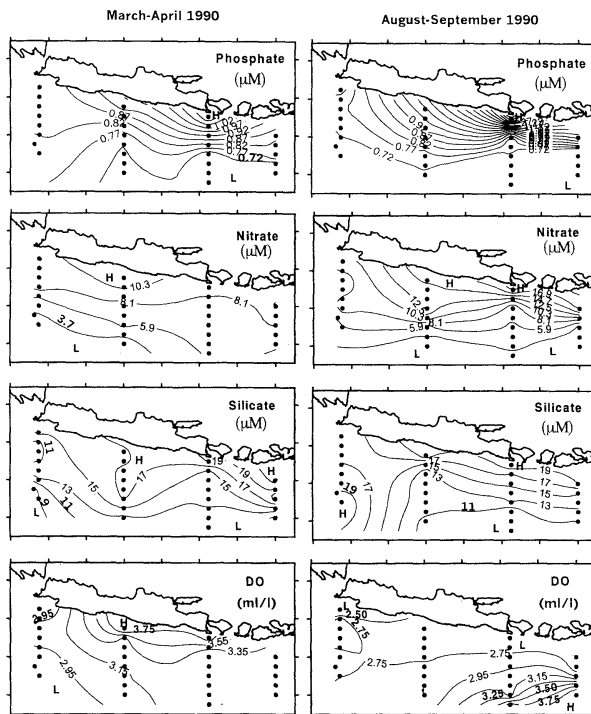


Fig. 4(b). Horizontal distributions of phosphate ($\mu\text{ mol/l}$), nitrate ($\mu\text{ mol/l}$), silicate ($\mu\text{ mol/l}$) and DO (ml/l) at 100 m depth.

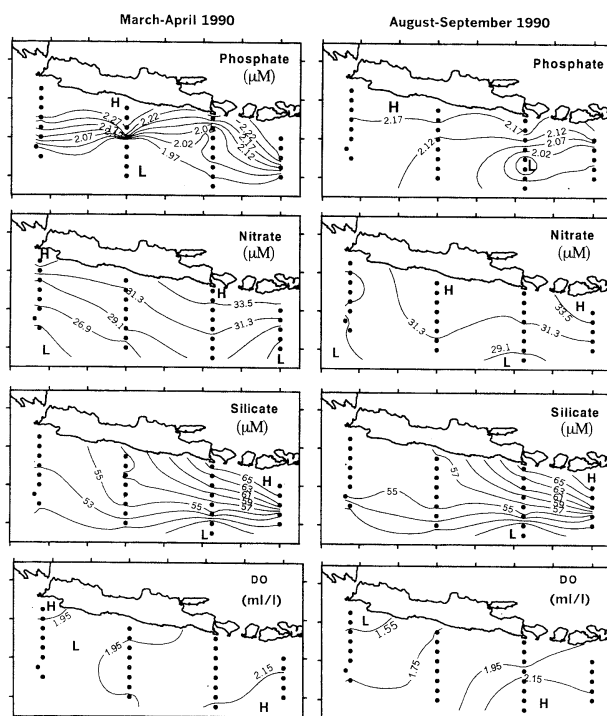


Fig. 4(c). Horizontal distributions of phosphate ($\mu\text{mol/l}$), nitrate ($\mu\text{mol/l}$), silicate ($\mu\text{mol/l}$) and DO (ml/l) at 500 m depth.

monsoon at the region of southern part of Bali to Sumbawa. At 100 m and 500 m depths, DO concentration in the southeast monsoon is slightly lower than that in the northwest monsoon. DO concentration at 100 m depth is within 2.50–3.75 ml/l in the southeast monsoon and 2.95–3.75 ml/l in the northwest monsoon.

Vertical distributions of phosphate, nitrate, silicate and DO along Legs 1 and 3 are shown in Figs. 5(a) and (b), respectively. At both Legs 1 and 3, phosphate, nitrate, silicate and DO are well stratified in both seasons. Large vertical gradient of phosphate, nitrate and silicate are seen between 50 to 350 m of both Legs 1 and 3. Along Leg. 3, higher phosphate, nitrate and silicate concentrations are seen to be migrated upward near shore as similar as DO during the southeast monsoon. The highest concentration of DO exists in the layer between 0–50 m depth.

3.3 Chlorophyll-*a*

Horizontal distributions of chlorophyll-*a* at the surface and 75 m depth are shown in Fig. 6. At the surface layer, chlorophyll-*a* in the

southeast monsoon is higher than that in the northwest monsoon. Chlorophyll-*a* is within 0.15–0.75 $\mu\text{g/l}$ in the southeast monsoon and 0.15–0.55 $\mu\text{g/l}$ in the northwest monsoon. High chlorophyll-*a* concentration in the southeast monsoon is concentrated at the near shore region of southern part of east Java and Bali, but in the northwest monsoon it is concentrated near shore region of west Java. At 75 m depth, however, concentration of chlorophyll-*a* in the southeast monsoon is lower than that in the northwest monsoon. Chlorophyll-*a* concentration in the southeast monsoon is within 0.15–0.45 $\mu\text{g/l}$ with high concentration at the near shore region of southern part of east Java to Bali. In the northwest monsoon, chlorophyll-*a* is within 0.25–0.75 $\mu\text{g/l}$ with high concentration at the near shore region of west Java.

Vertical distributions of chlorophyll-*a* along Legs 1 (western part) and 3 (eastern part) in the northwest and southeast monsoons are shown in Fig. 7. Along Leg 1, chlorophyll-*a* maximum is seen in the near shore region of west Java (Stas. 1–4) at 70–80 m depth in the

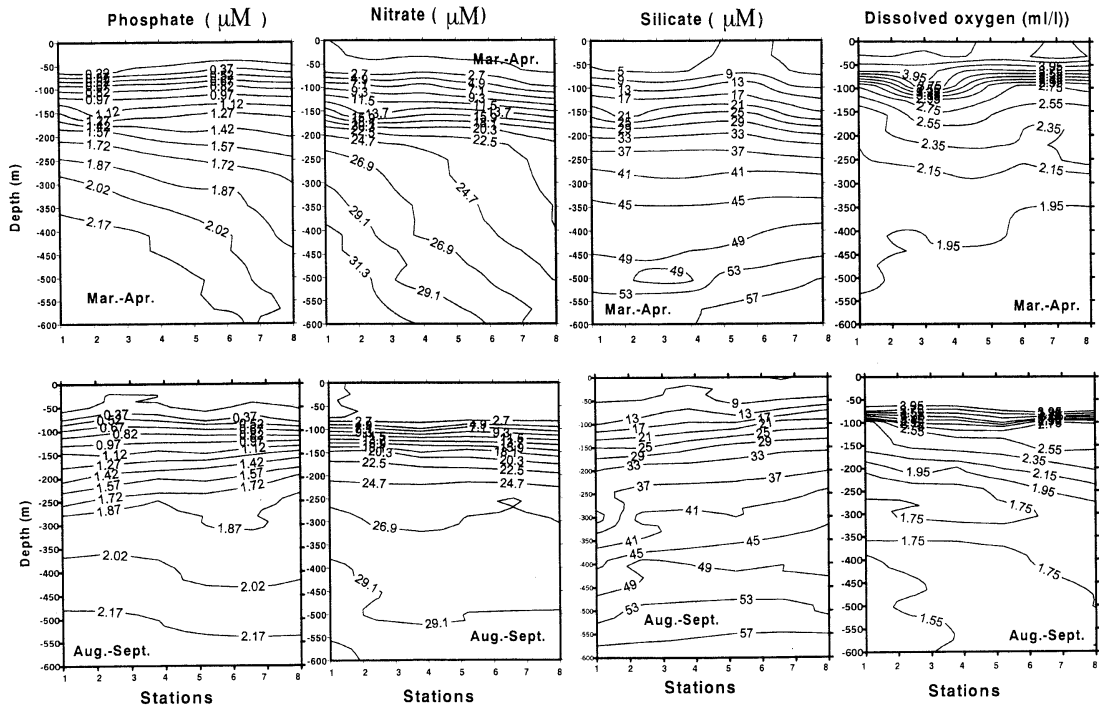


Fig. 5(a). Vertical distributions of phosphate ($\mu\text{ mol/l}$), nitrate ($\mu\text{ mol/l}$), silicate ($\mu\text{ mol/l}$) and DO (ml/l) along Leg. 1.

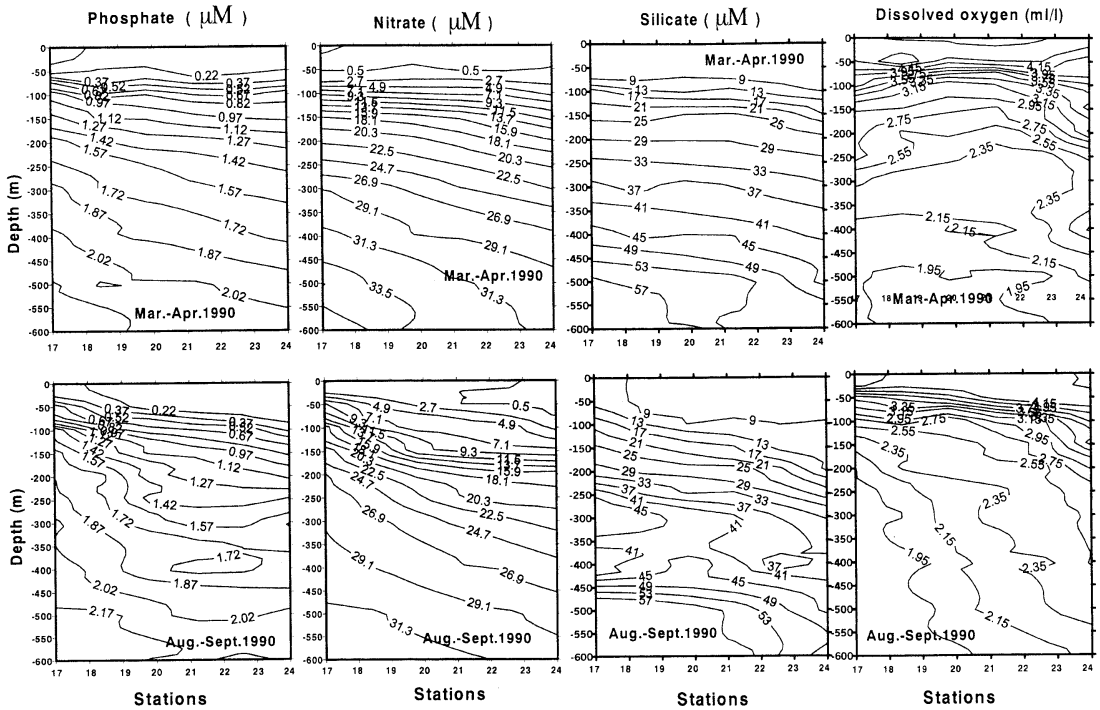


Fig. 5(b). Vertical distributions of phosphate ($\mu\text{ mol/l}$), nitrate ($\mu\text{ mol/l}$), silicate ($\mu\text{ mol/l}$) and DO (ml/l) along Leg. 3.

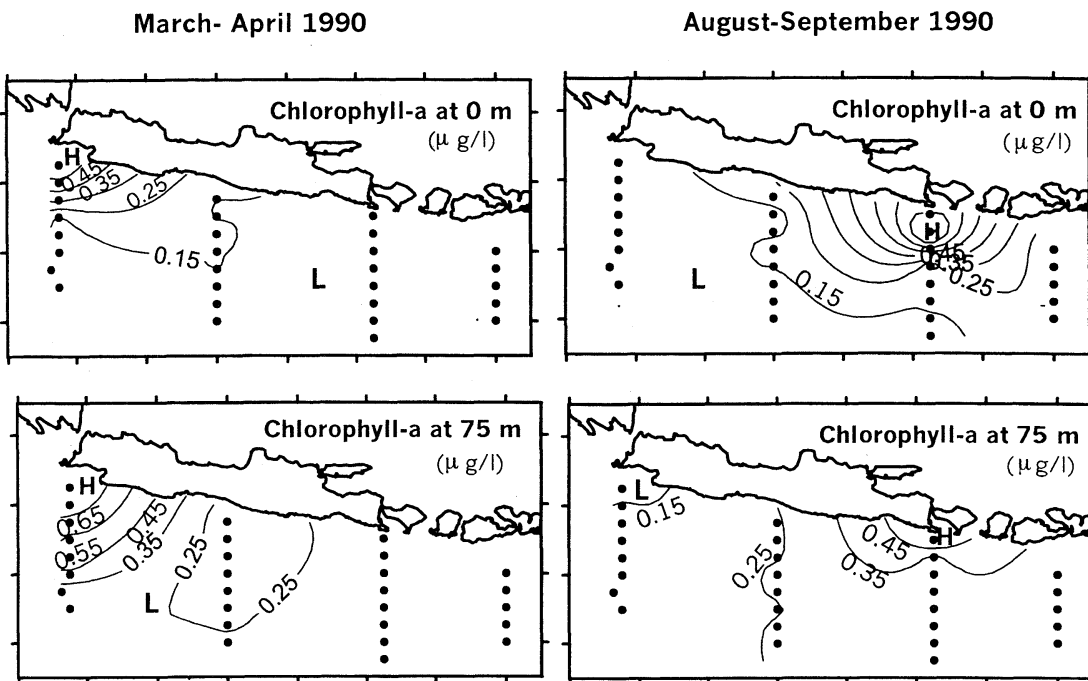


Fig. 6. Horizontal distributions of chlorophyll-a ($\mu\text{g/l}$) at the surface and 75m depth.

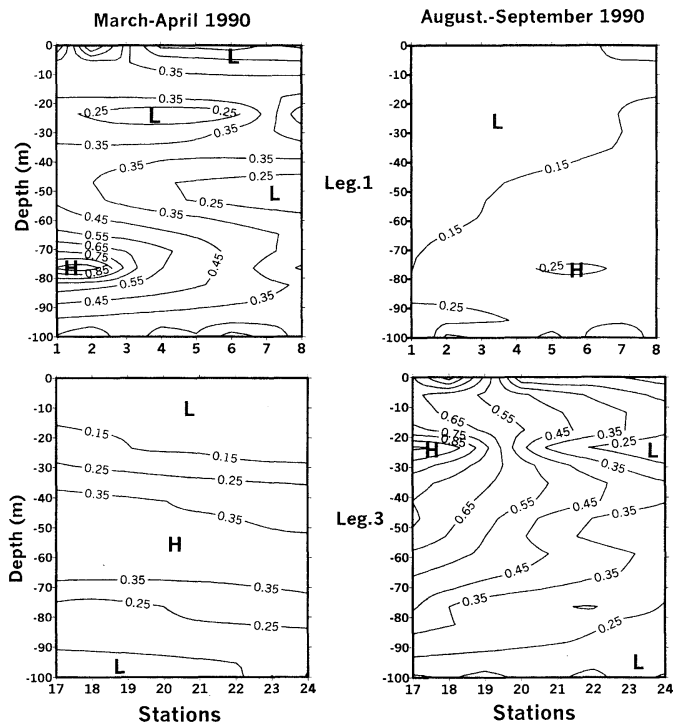


Fig. 7. Vertical distributions of chlorophyll-a ($\mu\text{g/l}$) along Legs. 1 and 3.

northwest monsoon. Along Leg. 3, chlorophyll-*a* maximum is concentrated in the near shore region of southern part of east Java (Stas. 17–20) at 20–30 m depth in the southeast monsoon.

4. Discussion

The oceanic condition along the southern part of Java to Sumbawa (Indian Ocean) is predominantly affected by the meteorological condition. T–S diagram shown in Fig. 8 strengthens this argument. The distributions of TS in both seasons are nearly the same except the upper part, that is, water temperature in the northwest monsoon (o) is higher by 1–3 °C than that in the southeast monsoon (+). Lower water temperature at the surface layer by 1–3 °C in the southeast monsoon shown in Fig. 2(a) is due to the upwelling generated by the sea surface Ekman transport responding to the southeasterly wind shown in Fig. 9. The occurrence of this upwelling is clearly seen in the horizontal distributions of water temperature and nutrients at the surface and 100m depth shown in Figs. 2(a) and (b) and Figs. 4(a) and (b). Moreover, the subsurface cold water with rich nutrients also appears in the surface layer of near shore region of south Bali due to the upwelling. As shown in Figs. 3(b) and 5(b), the subsurface cold water with rich nutrients along Leg. 3 is seen ascending from 250 m depth to the surface. As consequence, nitrate at the surface and 100 m depth is also increased even more than two times. This situation well agrees with the result of WYRTKI (1962), where the low temperature water mass with high phosphate concentration ascended to the surface from the subsurface layer (200 m). Such condition has generated phytoplankton bloom in the eastern part (Leg. 3) as indicated by chlorophyll-*a* increment at the surface and at 15–75 m depth (Figs. 6 and 7). Nutrients and chlorophyll-*a* are increased, but DO concentration at the surface and 100m depth is almost the same in the southeast monsoon and the northwest monsoon. This situation suggests that photosynthetic activity is low during the upwelling event due to low water temperature.

On the other hand, the distributions of physical and chemical parameters as well as DO at 500m depth show the similar situation between

the seasons as shown in Figs. 2(c) and 4(c). This situation indicates that water mass in this layer is stable than those at the surface and 100m depth. In addition, water temperature and salinity are higher in the western part (Leg. 1) than those in the eastern part (Leg. 3) in both seasons. This indicates that a warm and saline water mass is transported eastward from the Indian Equatorial Water.

Higher nutrient concentration at the surface and 100 m depth shown in Figs. 4(a) and (b) in both seasons tends to appear at the near shore region of Bali and spreads to the southwestern part (Leg. 1). This condition may be occurred due to the combined effect of tidal mixing in Bali and Lombok straits and the upwelling generated by southeasterly wind.

The oceanic condition in the southern coastal area of Java to Sumbawa shows a specific variability. Lower salinity and density at the surface layer in the western part (Leg. 1), especially at the near shore region of west Java in the northwest monsoon, is probably due to large river discharge generated by high precipitation (SACHOEMAR and YANAGI, 1999, SACHOEMAR and YANAGI, 2000). This situation, however, does not reach to the lower more than 50m depth and no significant effect on the increasing of nutrients concentration at the surface layer as shown in Figs. 2(a) and 5(a), though high concentration of chlorophyll-*a* at the surface layer is obviously seen at this area (Fig. 6).

Different situation is seen at the eastern part (Leg. 3) in the southeast monsoon where chlorophyll-*a* maximum is found at 20–30 m depth (Fig. 7) as similar as high nutrient concentration as shown in Fig. 5(b). This condition indicates that the upwelling is being occurred at the eastern part (Leg. 3) in the southeast monsoon which is also confirmed by highest chlorophyll-*a* concentration and low water temperature at the surface layer of Sta.18 in Fig. 9. The Rossby's internal deformation length (Lx) along Leg. 3 is calculated by the following formula:

$$Lx = \frac{\sqrt{\frac{gh_1 h_2 \Delta \rho}{\rho H}}}{f} \dots \dots \dots (1)$$

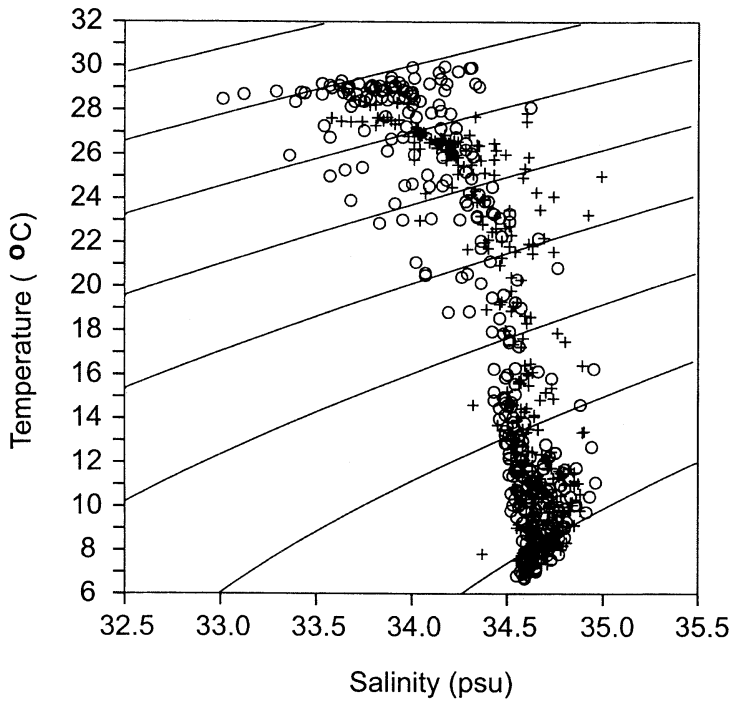


Fig. 8. T-S diagram in the northwest monsoon (o) and in the southeast monsoon (+).

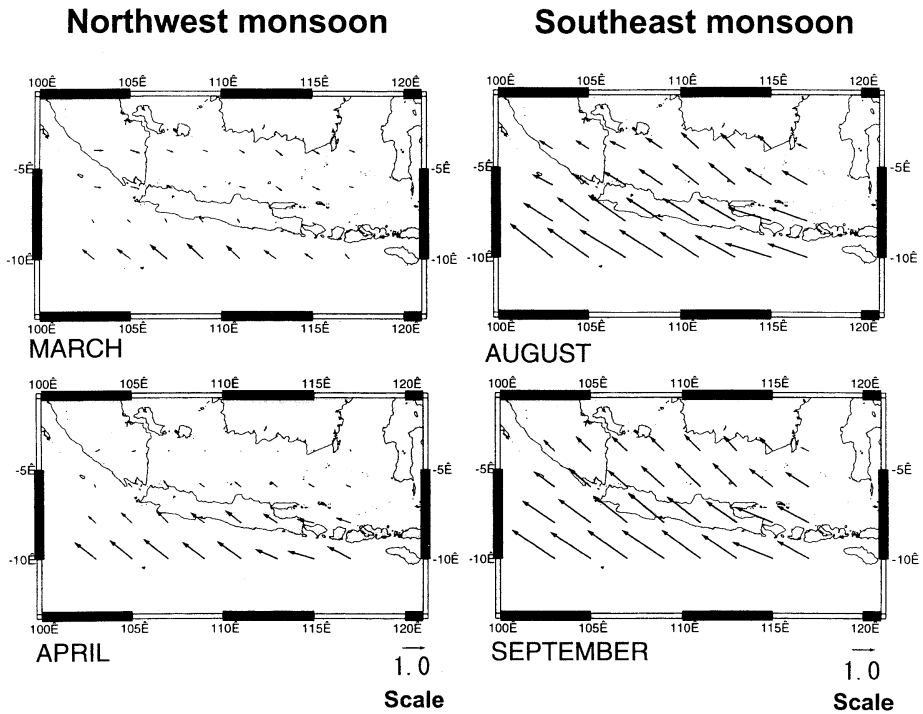


Fig. 9. Monthly mean wind stress (dyne/cm²) around Java to Sumbawa derived from the data in the period of 1870-1976 (Hellerman and Rosenstein, 1983).

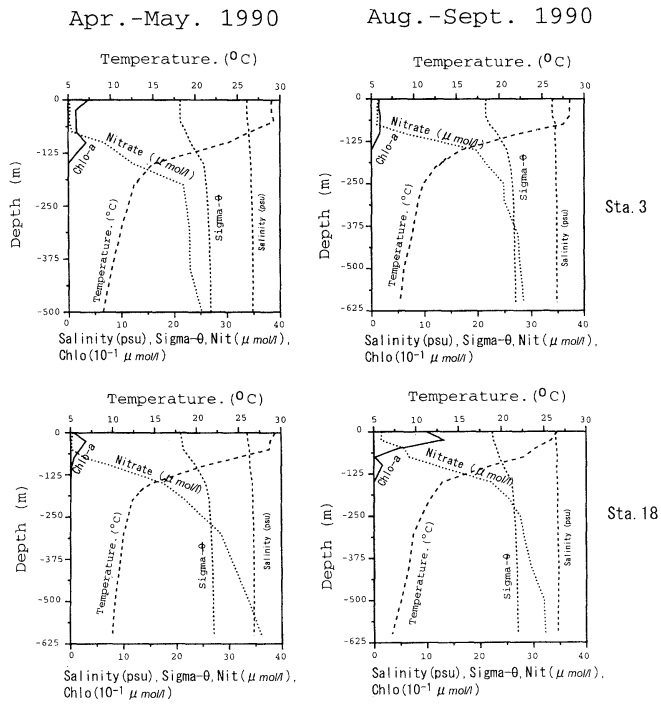


Fig. 10. Vertical profiles of water temperature (°C), salinity (psu), sigma-θ, nitrate (μmol/l), and chlorophyll-a (μg/l) at Stas. 3 and 18 in the northwest and southeast monsoons.

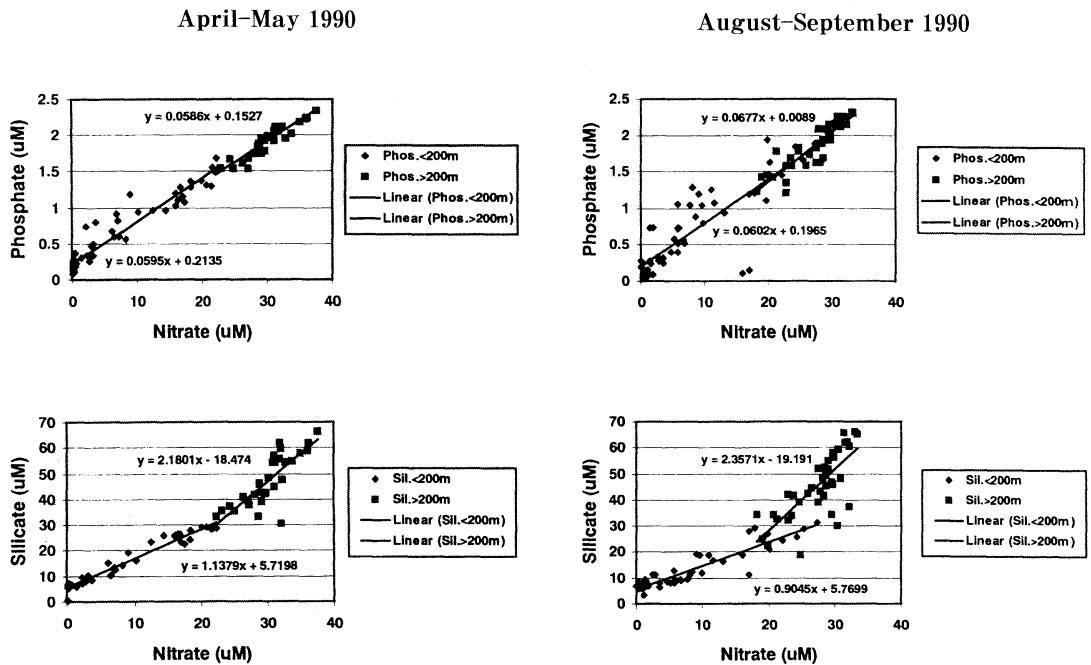


Fig. 11. Correlation of phosphate (μM) and silicate (μM) with nitrate (μM) during the northwest monsoon (April-May 1990) and the southeast monsoon (August-September 1990).

where g ($=9.8 \text{ ms}^{-2}$) denotes the gravitational acceleration, h_1 ($=100 \text{ m}$) and h_2 ($=900 \text{ m}$) the thickness of the upper and lower layers, respectively, H ($=100 \text{ m}$) the water depth, $\Delta\rho$ ($=0.003$) the density difference between the upper and lower layers and ρ ($=1.027$) the density in the lower layer and f ($=2.5 \times 10^{-3} \text{ s}^{-1}$) the Coriolis parameter from Fig. 10. The width of the upwelling along Leg. 3 estimated from Equation (1) is about 65km from the coast, which corresponds to the width of low water temperature area (Fig. 2b) and high chlorophyll-*a* (Fig. 6) area along Leg. 3 during the southeast monsoon.

Observational results also denote that nitrate concentration in the surface and 100m depth shown in Figs. 4(a) and (b) are significantly different between both seasons, that is, nitrate concentration is high during the upwelling event in the southeast monsoon. Moreover, nitrate seems to be a limiting factor for photosynthesis within this region because observed N/P ratio of 2–10 in the surface and subsurface layers for both seasons is smaller than the Redfield ratio of 16 and nitrate in the surface and subsurface layers (the depth less than 200m) is completely consumed by phytoplankton for photosynthesis, though phosphate and silicate are remained (Fig.11).

4. Conclusion

Variability of the oceanic condition along the southern coastal area of Java to Sumbawa is strongly affected by the meteorological condition corresponding to the seasonal change of monsoon. The southeast monsoon has generated the upwelling at the eastern part of the observational area. This situation has decreased water temperature at the surface layer up to 26°C and increased nitrate as well as chlorophyll-*a* significantly more than two times compared to those in the northwest monsoon. The oceanic condition at the surface layer up to 100m depth is more dynamic than that at 500m depth. Low salinity and density water mass due to the effect of high precipitation exists at the area of the western part in the northwest monsoon and it also has increased nutrient concentration which ultimately generates

phytoplankton bloom at the surface and 75m depth. Nitrate seems to be a limiting factor for photosynthesis within this region.

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日仏海洋学会賞受賞記念講演
肉食プランクトン，毛顎動物の生態学的研究*

寺崎 誠**

Ecological Studies on Carnivorous Plankton, Chaetognatha*

Makoto TREAZAKI**

このたびは伝統ある日仏海洋学会賞をいただき、まことに光栄に存じます。これを励みに生物海洋学のさらなる発展のために、これからも一層の努力をしたいと考えております。

私が故丸茂隆三先生のご指導で、東京大学海洋研究所プランクトン部門で毛顎動物の生態についての研究に取り組みしたのは1968年です。以来多くの皆様の温かいご支援を得て、この研究を今日まで継続する事ができましたのは、本当に幸せであると実感しております。本日は太平洋での研究を中心に肉食プランクトン，毛顎動物の分布，生活史および摂餌生態について報告させていただきます。

毛顎動物（矢虫類）は雌雄同体で世界の海洋に棲息し、全動物プランクトンの生物量の1～2割を占め、カイアシ類に次いで重要なグループである。典型的な肉食プランクトンでカイアシ類，オキアミ類などを主要な餌生物とし、時にはイワシ，ニシンなど有用水産資源の仔稚魚を捕食する（TERAZAKI, 2000）。また種によっては狭い水温・塩分の範囲にしか生息できないので水塊の指標生物として利用されている。

日本近海に出現する浮遊性毛顎類は次の5属32種である（寺崎, 1996）。

表層類 (21) :

Sagitta bedoti, *S. bipunctata*, *S. crassa*, *S. delicata*, *S. elegans*, *S. enflata*, *S. ferox*, *S. hexaptera*, *S. izuensis*, *S. minima*, *S. nagae*, *S. neglecta*, *S. pacifica*, *S. pseudoserr-*

atodentata, *S. pulchra*, *S. regularis*, *S. robusta*, *S. tumida*, *Pterosagitta draco*, *Krohnhitta pacifica*, *K. subtilis*

中深層種 (9) :

S. decipiens, *S. lyra*, *S. macrocephala*, *S. neodecipiens*, *S. scrippsae*, *S. zetesios*, *Eukrohnia hamata* (亜寒帯域では表層にも出現), *E. bathypelagica*, *E. fowleri*

1965年に相模湾および本州南方海域の1,000m以深より採集され、新種として発表された*Heterokrohnia bathybia* (MARUMO and KITOU, 1966) は、それ以降まだ出現していない。東京湾口の中層には*Eukrohnia kitoui* (KURODA, 1981) が生息しているが、まだ他の海域からは報告されていない。日本近海に出現する毛顎類は沿岸，外洋を問わず南の方が多い。

分布と鉛直移動

E. hamata は世界の大洋に生息し、亜寒帯水域，南大洋のような高緯度は表層に分布し、量的にも多く卓越したヤムシ類 (TERAZAKI, 1989; TERAZAKI and MILLER, 1986) であるが、低緯度に向かうにしたがって分布層は深くなり出現個体数も減少し、太平洋赤道水域では500m以深に生息する (ALVARIÑO, 1965)。*E. fowleri* は世界の大洋の700m以深の深層に分布するが、分布密度は1個体/1000m³以下と少ない。しかし湧昇があり、表層の生産が高いインド洋のアラビア海，ベンガル湾などでは30個体/1000m³という高い値を示した (TERAZAKI, 1999)。

S. elegans は沿岸から沖合いまで分布するが、春季，三陸沖を南下する親潮第一分岐では成体は沖合水の100m層に多く生息し，沿岸域にはほとんど出現しない (寺崎他, 1985)。*S. elegans* の分布の南限は太平洋では相模湾，日本海では対馬海峡である (MARUMO, 1966; TERAZAKI, 1998)。日本海からは3属16種のヤムシ類が

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報告されているが、中深層種が欠落している（鬼頭, 1974）。太平洋とつながる5つの海峡がいずれも130mより浅いため太平洋から中深層種の浸入がなく、逆に約1万年以前に北の宗谷海峡、津軽海峡から流入した表層種の*S. elegans*が徐々に深海生活に適応し、3000mまで生息するようになった。中深層に*E. bathypelagica*, *E. fowleri*, *S. macrocephala*のような競合種が存在しなかったのも日本海固有水内で分布層の拡大を容易にしたと考えられる（TERAZAKI, 1993a）。

三陸沖の移行域（混合水域）からは20種の毛顎類が報告されているが（鬼頭, 1974）、頻度がいずれかの季節に60%を越す種類は4種である。周年頻度が高いのは*S. minima*のみで、*S. nagae*は冬53%に低下するが、そのほかの季節では80%を越す。夏から秋にかけて頻度が高くのあるのは*S. enflata*と*S. regularis*である。冷水種の*S. elegans*は春と夏に頻度の上昇があるが、40%を越さない。

三陸沖には発生した、暖水塊86Bの調査では、4属19種の毛顎類が採集され、出現個体数は表層（0-200m）では暖水塊のフロント域で2500個体/1000m³と一番多く中心に向かうに従って激減していった（TERAZAKI, 1992）。暖水塊に多く出現するのは*S. scrippsae*, *S. minima*, *S. nagae*の3種で、冷水種の*S. elegans*, *Eukrohnia hamata*は暖水塊周辺のフロント域には多く生息するが、暖水塊中にはほとんどいなかった。86Bの起源は黒潮から分離した水塊にもかかわらず*S. enflata*, *S. regularis*, *S. pacifica*などの暖水種は量的に少なく、かつ中心部に向かうに従って出現個体数は減少していった（寺崎, 1998）。

86B暖水塊の深さは中央では約300mで水深50m以浅は顕著な水温・塩分躍層が発達し、表面には高水温（21°C）、低塩分（34.0 PSU）が存在した。9月には*S. nagae*, *S. minima*, *S. enflata*, *S. regularis*, *S. scrippsae*の5種は中央では昼夜を問わず100m以浅に生息していた。*S. scrippsae*は表面から300mに分布し、*S. lyra*, *S. neodecipiens*は量的に少ないが、暖水塊とその下の中層水に生息していた。*S. elegans*, *S. zetesios*, *E. hamata*, *K. subtilis*は主に中層水に分布しているが、小数は暖水塊の下層に出現した。*S. elegans*は鉛直移動によって暖水塊の中層水より中央水域の表面にも出現するが、躍層上には高水温、高塩分の表面水が春から秋にかけて存在するために、従来、低水温、低塩分で特徴づけられる親潮水に生息している*S. elegans*はこの環境に適応できずに死滅する（TERAZAKI, 1992）。

KURODA (1976)は黒潮域から22種の毛顎類を報告しているが、出現頻度からみて重要な10種は*S. minima*, *S. enflata*, *Pterosagitta draco*, *S. regularis*, *S. lyra*, *S. pacifica*, *S. nagae*, *S. hexaptera*, *Krohnia subtilis*, *S. pseudoserratodentata*の順であると報告している。特に*S. minima*は個体数の面で、冬夏ともに最も多い重要種である。*S. nagae*は、沿岸域において最多種ではないが、生態系の鍵種として、*P. draco*は沖合い域で重要種である。*S. lyra*, *S. pacifica*は黒潮域では冬季に、*S. enflata*と*S. regularis*は夏季に重要な種類である。ヤムシ類は水塊の指標生物として利用されるが南大洋オーストラリア区では亜熱帯収束線、南極収束線はヤムシ類の分布特性とも深い関連性を持っていた（TERAZAKI, 1989）。表層種の*S. elegans*, *S. nagae*のみならず*E. hamata*や*S. zetesios*のような中深層種でも成熟した個体は未熟個体より深い層に生息していた（TERAZAKI and MARUMO, 1982）。

表層種の*S. elegans*, *S. minima*, *S. nagae*, *S. pacifica*, *K. subtilis*などでは顕著な昼夜鉛直移動をすることが知られている（KOTORI, 1976; KING, 1979; 永沢・丸茂, 1982）。*S. elegans*は夜は表面近くに分布するが、昼は深い層まで下降する。一日の移動幅は大型の個体ほど大きく、45°N, 160°10'Eに生息する*S. elegans*の成体の時間当たりの上昇・下降速度は約30mであり、ときには水温躍層を越えて昼夜移動することもある（TERAZAKI and MARUMO, 1979）。ヤムシ類の眼構造は生息深度により異なり表層種は大きな眼色素を持つが、中深層種では色素は小さいか欠落しており、逆に光受容体は表層種より発達していた（GOTO *et al.*, 1989）。

生活史

底生性の*Spadella*はいつでも産卵し、特に夜にピークをもつことが知られているが（GHIRARDELLI, 1968）、日本近海では*S. elegans*や*S. nagae*も夜に産卵する（KOTORI, 1975; 永沢・丸茂, 1978）。受精卵の大きさは*S. elegans*では0.3~0.33mm（ZO, 1973; KOTORI, 1975）、*S. hispida*では0.2mm（REEVE and COSPER, 1975）、*S. nagae*では0.16~0.2mm（永沢・丸茂, 1978）、*P. draco*（SHIMOTORI *et al.*, 1997）では0.3mmあったが、これに対して*E. bathypelagica*, *E. fowleri*では0.48mm, 0.9mm（TERAZAKI and MILLER, 1982）で前記の表層種に比べてかなり大きい。孵化直後の仔虫の大きさは*S. bipunctata*, 1mm（DONCASTER, 1902）、*S. crassa*, 0.7mm（村上, 1959）、*S. elegans*, 1.2~1.4mm

(KOTORI, 1975), *S. nagae*, 0.5~0.6 mm (永沢・丸茂, 1978), *P. draco*, 1.24 mm (SHIMOTORI *et al.*, 1977), *E. bathypelagica*, 2.5 mm, *E. fowleri*, 3.0~3.5 mm (TERAZAKI and MILLER, 1982) である。*Sagitta* 属では受精卵は海中に放出されるのに対して *E. bathypelagica*, *E. fowleri* ではエッグサックの中に生み出され、この中で孵化し仔虫になるという過程をもつので、*Sagitta* 属に比べると生存率も高く、かつ深海生活への適応も容易であると考えられる。

表層種の産卵期については多くの報告がある (ALVARIÑO, 1965)。日本近海での *S. elegans* の産卵期は千島列島付近では4-5月 (TERAZAKI *et al.*, 1995)、釧路沖では春から秋、特に6-7月 (西内・池田, 1998)。北海道南方水域では5-6月 (KOTORI, 1999)、大槌湾では4月 (寺崎・丸茂, 1982)、富山湾では3-5月と8月である (TERAZAKI, 1993b)。水温が通年1度以下の富山湾の中層に生息する *S. elegans* の寿命は10-12月で、太平洋での Dabob Bay, Station P の報告 (KING, 1979; TERAZAKI and MILLER, 1986) より長い。KOTORI (1999) は釧路沖の親潮域に生息する *S. elegans* の寿命を1年以上と推定している。

典型的な三陸リアス式海岸の1つである大槌湾には年間9種の毛顎類が出現し、*S. crassa*, *S. enflata*, *S. minima*, *S. nagae* の産卵期はそれぞれ5-10月, 8-10月, 8-12月・2-5月と10-11月であるが、湾内で生活史を繰り返すのは、*S. crassa* と *S. minima* の2種である (寺崎・丸茂, 1982)。駿河湾の、*S. nagae* では1年を通して6つの同時発生集団 (コーホート) が存在し、各コーホートの寿命は3, 5, 7カ月に春~夏のコーホートの一生は最も短く、夏の終わりに生まれるコーホートの一生が最も長い (永沢・丸茂, 1978)。ノルウェーの Krsfjorden では *E. hamata* は卓越種であり、春から秋にかけて産卵し、その寿命は約2年で春から夏にかけての成長は4 mm/月であった (SAND, 1980)。

北太平洋アラスカ湾のP点に出現する *E. hamata* は1年に3つのコーホートが存在し、それぞれの寿命は8-9カ月に、平均成長速度は2.5~3 mm/月であった (TERAZAKI and MILLER, 1986)。またP点では *E. bathypelagica* と *E. fowleri* は周年産卵を行う。

摂餌生態

太平洋の外洋表層では *S. elegans* と *E. hamata* の生息層は競合するが、*S. elegans* は主に *Neocalanus*, *Metridia* などの大型カイアシ類、より深い層に棲む *E.*

hamata は *Oithona* などの小型カイアシ類を捕食し、いわゆる喰い分け現象が報告されている (SULLIVAN, 1980)。しかし沿岸域に生息する *S. elegans* にとっては *Acartia*, *Oithona*, *pseudocalanus* などの小型カイアシ類が主要な餌である (TERAZAKI, 1995)。*S. elegans* はカイアシ類の他にオキアミ類、端脚類、介形類、稚仔魚などを捕食し、時には共食いも見られる (TERAZAKI, 2000)。1997年夏季の調査では *S. elegans* の摂餌活動はベーリング海で高く、東部北太平洋 亜寒帯水域で低かった (MATSUDA and TANIGUCHI, 2001)。SAMEOTO (1973) によると、カナダの Nova Scotia ではカイアシ類の年間生産の36%は *S. elegans* によって消費される。夏季のベーリング海では1日に2次生産量の約10%が *S. elegans* によって消費されると報告されているが (KOTORI, 1976)、アリューシャン列島以南では摂餌活動は日没から夜間にかけて活発で、毎日、2次生産量の約4%を消費していた (TERAZAKI, 1995)。

日本海の *S. elegans* の摂餌活動は昼夜の差がほとんどなく、太平洋に比べるとより大型の餌を捕食していた。また顎毛、歯などの餌捕獲器官や消化管周辺組織も深海生活に適應するため太平洋の個体より発達していた (TERAZAKI, 1993a)。

駿河湾、相模湾の卓越種 *S. nagae* の主要な餌は水層および近底層で卓越するカイアシ類 *Calanus pacificus* であり、水層では昼より夜に、近底層では夜より昼に活発に摂餌し、カイアシ類の大きさの違いによる選択性を示さなかった。また *S. nagae* は水層と近底層の間を移動し、沿岸浅所の食物連鎖において重要な役割を果たしている (NAGASAWA and MARUMO, 1976)。また *S. nagae* の1日当たりの食物要求量は乾重量ベースで自体重の39.5%であった。

ハワイの Kaneohe 湾では *S. enflata* は体長とは無関係にほぼ等しい餌保有率を示し、1日当たり平均7個体のカイアシ類を捕食していた (SZYPER, 1978)。しかし FEIGENBAUM (1979) によるとメキシコ湾流中の *S. enflata* では餌保有率は体長によって有為な差があり、1日平均2.2個体のカイアシ類を捕食していた。太平洋中部赤道海域に生息する *S. enflata* は50 m 以浅の表層上部では夜間、表層下部では昼間に活発な摂餌を行い、2次生産量の約8%を消費していた (TERAZAKI, 1996)。NEWBURY (1978) によると *P. draco* は1日当たり1個体の小型カイアシ類 *Oncaea* を捕食するが、これは窒素量ベースで自体重の2%に相当する。

相模湾の中深層に生息する *S. zetesios* の摂餌活動は

昼の方が活発で、24種のカイアシ類、5種のヤムシ類、1種の介形類を捕食していたが、このうち10種は表層性のプランクトンで、*S. zetesios* は日中に鉛直移動で表層から下降してきたカイアシ類、矢虫類などを活発に捕獲することが明らかにされた (TERAZAKI and MARUMO, 1982)。

S. setosa と *S. elegans* に稚魚とカイアシ類を与えて24時間の飼育実験を行った結果、摂餌と体長の間には明瞭な関係はなく、どの体長のヤムシも平均1.8個体のカイアシ類、あるいは0.3個体の稚魚を捕食していた (KUHLMANN, 1977)。餌の密度と捕食の関係については *S. elegans*, *S. hispida*, *S. setosa* で報告されている。KUHLMANN (1977) は1~50個体/Lの密度をカイアシ類を *S. elegans* に与えた実験では、餌生物の密度はヤムシの捕食に影響を与えないという結論を得たが、*S. hispida* を用いて実験を行った FEIGENBAUM and REEVE (1977) は、20個体/Lの密度までは餌の密度が大きくなるに従って摂餌も増加すると述べている。

通常、生きたヤムシの体色は無色透明であるか乳白色である。しかし深海に生息する *S. macrocephala* や *E. fowleri* の消化管、時には東部、鰭は紅橙色を呈している。従来、この色は餌として食べられたカイアシ類の体色が直接、消化管についたものと考えられていたが (ALVARINO, 1965; 時岡, 1965), TERAZAKI *et al.* (1977) はクロマトグラフ分析でこの色素はカロテノイド色素で、餌由来のものではなく、毛顎動物自体の体内で生合成されたものであることを明らかにした。

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資 料

第 39 卷第 3 号掲載欧文論文要旨

Yan ROBERT-COUDERT*・加藤明子*・内藤靖彦* : 海洋高次捕食者の採餌行動の再構築

南大洋の海鳥や海産哺乳類などの高次捕食者は多量の海洋資源を消費しており、同じく海洋資源を利用している漁業活動と相互作用がある。したがってこれらの捕食者の採餌行動の情報を集めることは非常に重要だが、海洋での行動を直接調べることは困難である。研究者は近年、連続的に様々なパラメータを記録するマイクロデータロガーを海洋捕食者に装着してきた。その結果、海鳥や海産哺乳類の海での採餌行動を直接的に計測することが可能になり、これらの捕食者の体内温度を計測することも可能となった。最近、海鳥の食道上部の温度を他のパラメーターと共に計測することに成功した。本稿では海洋における高次捕食者の採餌行動を計測するためのさまざまな方法についてレビューした後、体内温度（特に食道温度について）の計測結果と海鳥および海産哺乳類の採餌行動研究におけるその有用性について論議した。（*国立極地研究所 〒173-8515 板橋区加賀1-9-10）

Boonyarath PRATOOMCHAT*・夏苺 豊・三木育子**・Kashane CHALERMWAT : 日本産およびタイ産アオリイカの遺伝的多様性のアロザイム分析**

長崎（日本）および Rayong（タイ）で捕獲されたアオリイカ（*Sepioteuthis lessoniana* Lesson, 1830）の地域個体群について、その遺伝的変異と個体群の遺伝子型構造を多遺伝子座アロザイム分析により調べた。スクリーンされた 22 遺伝子座にもとづいて決定された多型遺伝子座の割合と、観察された平均ヘテロ接合体率は日本の個体群でそれぞれ 45.45 % および 0.28、タイの個体群でそれぞれ 50.00 % および 0.23 であった。これらの結果は、アオリイカの個体群内での遺伝的多様性が相対的に高いことを示唆している。同時にまたこれらの個体群の間の遺伝的距離は低い（ $D=0.003$ ）ことが観察された。日本産およびタイ産のアオリイカ個体群間で遺伝的分化が欠けていることは、地理的に広範な地域に亘ってアオリイカの汎生殖遺伝子プールが存在することを示唆している。（*Department of Aquatic Science, Faculty of Science, Burapha University, Chonburi, 20131, Thailand,**長崎大学水産学部 〒852-8521 長崎市文教町1-14）

Suhendar I. SACHOEMAR*・柳 哲雄 : インドネシアジャワスンバウ南岸沿いにおける海況の季節変動**

ジャワスンバウ南岸沿いにおける海況の季節変動特性を明らかにするために、北西モンスーン（1990年4-5月）期と南東モンスーン（1990年8-9月）期に、現地調査を行った。観測は物理（水温、塩分）、化学（リン酸、硝酸、珪酸）、生物（クロロフィル *a*、溶存酸素）項目の水平・鉛直分布を明らかにした。海況変動は季節風に対応した降雨と湧昇の変動に依存していることが明らかになった。南東季節風時の沿岸湧昇により表層の栄養塩（特に硝酸）濃度は上昇し、水温は下降する。硝酸がこの海域の基礎生産の律速栄養塩になっている。（*九州大学大学院総合理工学府、**九州大学応用力学研究所 〒816-8580 福岡県春日市春日公園6-1）

学 会 記 事

1. 2001年5月27日(日) 日仏会館会議室において、平成13年度学術研究発表会が開かれた。発表題目と発表者は次の通り。

午前(9:40~12:00)

1. 太平洋3時次元流動解析の検討…○長谷川一幸・和田 明(日大)・高野憲治(コロンビア大)
2. 夏季の宗谷暖流の流速構造と流量…○松山優治・阿部泰三(東水大)・青田昌秋(北大)・和高牧子・小池義夫・喜多澤 彰・宮崎唯史・鈴木文枝(東水大)
3. 夏季の宗谷暖流の水温、塩分、密度構造について………○和高牧子・松山優治(東水大)・青田昌秋(北大)・小池義夫・喜多澤 彰・宮崎唯史・鈴木文枝(東水大)
4. 内浦湾における内部潮汐の鉛直構造
○川村有二・北出裕二郎・松山優治(東水大)
5. 南海トラフ周辺の海水位変動と地形変動
………○中村重久
6. 三宅島噴火に伴う降灰による周辺海域の海況への影響………○井桁庸介・松山優治(東水大)
7. 三宅島周辺海域の濁りの分布………○荒川久幸・小西晶子・森永 勤(東水大)

午後(13:20~15:00)

8. 学習法を用いたオオクチバスの視覚認識能力に関する研究—精度とコントラスト閾値について—
………○小田智則・平野真也・森川由隆(三重大)
9. 富津ノリ養殖漁場における光環境とノリ網の色彩について………○森永 勤・大久保べに・荒川久幸(東水大)
10. 西部北太平洋におけるネット動物プランクトンバイオマスおよび化学組成(WEST-COSMIC)
………○山口 篤・渡辺雄二・石田 洋・播本孝史・前田匡哉(関西総環センター)・石坂丞二(長崎大)・池田 勉(北大)・高橋正征(東大)
11. 秋サケ来遊群の動態解析………○長谷川英一・斎藤寿彦・広井 修(さけ、ます資管センター)
12. 画像解析によるヒラメの心拍数計測法
………○廣田 裕・矢田貞美・湯原隆行(東水大)

2. 2001年5月27日(日) 日仏会館会議室において、第42回(平成13年度)総会が開かれた。議事の概要は次の通り。

1) 平成12年度事業報告

(a) 庶務

会員移動状況

	平成12年 4月	入会	退会	逝去	資格変更	平成13年 3月
名誉会員	2	-	-	-	-	2
正会員	276	11	12	1	-	274
学生会員	2	1	-	-	-	3
賛助会員	14	-	1	-	-	13

(b) 活動状況

評議員会	1回
幹事会	4回
総会	1回
学術研究発表会	1回
学会誌発行	
学会賞授与	関 文威(筑波大学)

(c) 編集

学会誌 La mer 38(1), 38(2), 38(3), 39(1)刊行, 38(4)は10th PAMS/JECSS Workshopプロシーディングスとして別途編集

2) 平成13年度学会賞受賞候補者選考経過報告(詳細は3参照)

3) 平成12年度収支決算および監査報告

収 入	
前年度繰越金	175,1759
正会員会費	1,071,783
学生会員会費	4,000
賛助会員会費	170,000
学会誌売上金	213,943
広告料	60,000
別刷印刷費	238,800
著者負担印刷費	250,000
雑 収 入	49,909
寄 付 金 収 入	150,000
合 計	2,383,594

支 出

学会誌印刷費	1,250,000
送料・通信費	173,112

事 務 費	687,486
交 通 費	19,310
会 議 費	7,874
学 会 賞 経 費	73,166
雑 費	32,456

小 計	2,243,404
次 年 度 繰 越 金	140,190

合 計	2,383,594
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4) 平成13年度事業計画(案) 審議

下記原案通り承認された。

評議員会, 総会, 学術研究発表会および幹事会の開催
学会誌「La mer」の刊行

平成13年度学会賞授与および平成14年度受賞候補者の
推薦
その他

5) 平成13年度予算(案) 審議

原案通り承認された。

収 入	
前年度繰越金	140,190
正 会 員 会 費	1,644,000
学 生 会 員 会 費	12,000
賛 助 会 員 会 費	170,000
学 会 誌 売 上 金	300,000
広 告 料	60,000
別 刷 印 刷 費	300,000
著 者 負 担 印 刷 費	300,000
雑 収 入	50,000
寄 付 金 収 入	1

合 計	2,976,191
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支 出	
学 会 誌 印 刷 費	1,800,000
送 料 ・ 通 信 費	250,000
事 務 費	700,000
交 通 費	24,000
会 議 費	23,000
学 会 賞 経 費	75,000
雑 費	30,000
予 備 費	74,191

合 計	2,976,191
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6) その他

引き続き寺崎 誠会員への学会賞授与と受賞記念講演が行われた。また終了後アトレ恵比寿「桃花宮」で懇親会が開かれ、盛会裡に終了した。

3. 平成13年度日仏海洋学会賞

受賞者：寺崎 誠(東京大学海洋研究所)

受賞課題：肉食プランクトン, 毛顎動物の生態学的研究

推薦理由：毛顎動物(矢虫類)は雌雄同体で世界の海洋に棲息し, 全動物プランクトンの生物量の1~2割を占め, カイアシ類に次いで重要なグループである。典型的な肉食プランクトンでカイアシ類, オキアミ類などを主要な餌生物とし, 時にはイワシ, ニシンなど有用水産資源の仔稚魚を捕食する。また種によっては狭い水温・塩分の範囲にしか生息できないので, 水塊の指標生物として利用されている。毛顎動物の研究はこれまで内湾や沿岸域を中心に行われており, 深海を含む外洋域での知見が乏しいのが実情である。

寺崎 誠博士は1968年に外洋に生息する毛顎動物の生態についての研究に着手し, 以来, 今日に至るまで世界の諸水域で精力的に仕事を続けている。同博士は相模湾, 三陸沖, 日本海, 本州東方海域, オホーツク海, アラスカ湾, 中部熱帯太平洋, 南太平洋, インド洋で, 表層から深層にいたる毛顎動物の水平・鉛直分布を明らかにした。特に太平洋では, 亜寒帯水域の200 m以浅に生息しているキタヤムシが, 日本海に北方の海峡を経由で移入後, 徐々に深海適応し3000 mまで分布していることを明らかにした。また世界の大洋の700 m以深に生息し, 分布密度も低い(1個体/1000m³以下)深海赤クロンヤムシが, 湧昇の影響が強いアラビア海, ベンガル湾に多量(30個体以上)に出現するという新知見を得た。クロンヤムシは南極海, 北太平洋亜寒帯水域では表層下部, 中緯度では中層, 低緯度では100 m以深の深層に生息することを詳細な分布調査で確かめた。キタヤムシ, 沿岸ヤムシなど表層種の多くは, 顕著な昼夜鉛直移動を行い, 移動幅は外洋のキタヤムシでは幼体は, 10~20 m, 成体は約150 mであると報告した。相模湾の深海フトヤムシの幼体は, 500 m以浅の中層上部に生息するが, 成長に伴い分布深度が深くなり, 成体分布中心は深層にあった。

毛顎動物を水塊の指標として用いた研究は, 大槌湾, 三陸沖, 南大洋で行われた。大槌湾には9種の毛顎動物が出現するが, 親潮第一分岐の南下に伴い, 春にキタヤムシが湾内に流入するが, 水温上昇にともなって消滅し, 逆に沖合に断水の影響の強い夏~秋には, 黒潮系水の指標種フクラヤムシが流入し水温の下降する冬まで生残し, 湾内で生活史を繰り返すのは沿岸ヤムシとヒメヤムシの2種であることを明らかにした。

暖水塊には10種の毛顎動物が出現したが、これらの個体数は縁辺部で多く、中心に向かうに従い激減し、冷水種キタヤムシは縁辺部と水塊底部に多く生息し、鉛直移動により水塊内に侵入するが生残できないことが解明された。南大洋オーストラリア区では、亜熱帯収束線および南極収束線は毛顎動物の分布特性とも深い関連性を持つことを検証した。

同博士は生活史についても多くの知見を得ており、特にアラスカ湾の定点Pでの研究で、深海クローンヤムシ、深海赤クローンヤムシは体に付着したエッグサックの中に受精卵を生み出し、この中で孵化し仔虫になるという過程を持つという貴重な発見をした。仔虫はそれぞれ2.5 mm, 3.5 mmの大きさで膜を被って出るので、卵の状態に比べて深海生活への適応も容易である。黒潮系水の表層に生息するヘラガタヤムシの孵化直後の体長は1.24 mmで、2日目には顎毛や眼色素が認められた。定点Pではキタヤムシ、クローンヤムシともに3つの産卵期をもち、寿命は6~10カ月、8~10カ月で成長速度は約5 mm/月、3 mm/月であった。富山湾、大槌湾および道南海域のキタヤムシは、生息環境条件が異なっているにもかかわらず主産卵期は3~5月で、富山湾での寿命は10~12カ月であった。

生息海域、種を問わず、毛顎動物の主要な餌生物はカイアシ類であり、通常、消化管内容物の50%以上を占めた。西部北太平洋のキタヤムシの摂餌活動は日没から夜間にかけて活発で、毎日、2次生産量の4%を消費していた。日本海のキタヤムシの摂餌活動は、昼夜の差がほとんどなく、太平洋に比べるとより大型の餌を捕食していた。また顎毛、歯などの餌捕獲器官や消化管周辺組織も深海生活に適応するため太平洋の個体より発達していた。太平洋中部赤道海域に生息するフクラヤムシは、50 m以浅の表層上部では夜間、表層下部では昼間に活発な摂餌を行い、2次生産量の約8%を消費していた。相模湾の表層から下降してきたカイアシ類、矢虫類を多く捕食していた。深海の毛顎動物の中には消化管を中心に紅橙色を呈した種類がいるが、寺崎博士は黒間とグラフ分析でこの色素はカロテノイド色素で、餌由来のものではなく、毛顎動物自身の体内で生合成されたものであることを明らかにした。

脆弱な体をもち採集が困難な毛顎動物、サルバ類、クラゲ類を効率よく、損傷もなく定量的に採集するため、1986年以降、3種類の鉛直多層式ネットを開発した。このネットを用いれば6000 mから層別採集も可能で、現在、大学、水産庁、企業で汎用されている。

以上、一連の研究は、外洋、深海での毛顎動物の生態について多くの新知見を提供し、海洋生態系における肉食プランクトンの役割について解明した。寺崎博士の業績は国内外で高く評価されており、これまで多くの図鑑、本の分担執筆を依頼され、1993年には世界

毛顎動物研究会の推薦で米国スミソニアン協会の自然史博物館の所有する膨大な毛顎動物試料の評価、査定を行った。

本委員会は同博士の研究が生物海洋学の進展に寄与するところが顕著であり、本学会賞の授与にふさわしいものとしてここに推薦する。

学会賞受賞候補者推薦委員会
委員長 青木三郎

主要論文

- 1) Pigment of meso- and bathypelagic chaetognaths. *Mar. Biol.*, **41**: 119-125 (1977). (with R. Marumo and Y. Fujita)
- 2) Diurnal vertical migration of *Sagitta elegans* Verrill in the Western North Pacific Ocean. *Bull. Plankton Soc. Japan.* **26**: 11-17 (1979). (with R. Marumo)
- 3) Feeding habits of meso- and bathypelagic chaetognaths, *Sagitta zetesios* Fowler. *Oceanol. Acta*, **5**: 461-464 (1982). (with R. Marumo)
- 4) Reproduction of meso- and bathypelagic chaetognaths in the Genus *Eukrohnia*. *Mar. Biol.* **71**: 193-196 (1982). (with C. B. Miller)
- 5) 大槌湾における毛顎類の性状と海況変動の関係. *日仏海洋学会誌*, **20**: 111-117 (1982). (丸茂と共著)
- 6) 親潮接岸期における大槌湾周辺の毛顎類の鉛直分布. *大槌臨海研究センター報告*, **11**: 1-7 (1985). (北川・山下と共著)
- 7) Life history and vertical distribution of pelagic chaetognaths at Ocean Station P in the subarctic Pacific. *Deep-Sea Res.*, **33**: 323-337 (1986). (with C. B. Miller)
- 8) Examination of the possibility of automated identification of Chaetognatha utilizing an image processor. *Bull. Plankton Soc. Japan.* **33**: 95-100 (1986). (with T. Ishii)
- 9) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeo-chemical structure of the food web. *Deep-Sea Res.* **34**: 829-841 (1987). (with E. Wada, Y. Kabaya and T. Nemoto)
- 10) Colour Pattern of *Spadella angulata* (Chaetognatha: Spadellidae) with a Note on Its Northern Range Extension. *Bull. Plankton Soc. Japan.* **34**: 83-84 (1987). (with R. Bieri, E. Thusen and T. Nemoto)
- 11) The comparative morphology of the eyes of the Genus *Sagitta* Ghaetognath). *Exp. Biol.* **48**: 95-105 (1989). (with T. Goto and M. Yoshida)
- 12) Distribution of chaetognaths in the Australian Sector of the Southern Ocean during the BIOMASS SIBEX Cruise (KH-83-4). *Proc. NIPR Symp. Polar*

Biol.: 2, 51-60 (1989).

13) Deep - Sea Chaetognaths, *In: Biology of Chaetognatha*, Q. Bone et al. (editor), Oxford Univ. Press, Oxford, 117-121 (1991).

14) Horizontal and vertical distribution of chaetognaths in a Kuroshio Warm-Cor Ring. *Deep Sea Res.*, **39**, Suppl. 1: 231-245 (1992).

15) Seasonal variation and life history of the pelagic chaetognatha, *Sagitta elegans* Verrill in Toyama Bay, southern japan Sea. *J. Plankton Res.* **15**: 703-714 (1993).

16) Deep sea adaptation of epipelagic chaetognatha *Sagitta elegans* in the Japan Sea. *Mar. Ecol. Prog. Ser.* **98**: 79-88 (1993).

17) Horizontal distribution and seasonal change of epipelagic chaetognatha *Sagitta elegans* in relation to arounds the Kurile and Hokkaido Islands in the western subarctic Pacific Ocean. *Fish. Oceanogr.*: **4**, 158-170 (1995). (with H. Saito, H. Kasai, T. Kono, Y. Kawasaki and T. Taguchi)

18) The role of carnivorous zooplankton, particularly chaetognaths in ocean flux. *In: Biogeochemical Processes and Ocean Flux in the Western Pacific*. Sakai, H. and Y. Nozaki(editor), TERAPUB, Tokyo, 319-330 (1995).

19) Vertical distribution and feeding of pelagic chaetognaths and feeding of *Sagitta elegans* in the central Pacific Equatorial Water. *J. Plankton Res.* **18**: 673-682 (1996).

20) Egg colony and early development of *Pterosagitta draco* (Chaetognatha) collected from Kuroshio front. *Plankton Biol. Ecol.* **44**, 71-80 (1997). (with T. Shimotori and T. Goto)

21) A Vertical Multiple Opening Closing Plankton Sampler. *J. Adv. Mar. Sci. Tech. Soci.*: **3**- 1-10 (1997). (with C. Tomatsu)

22) Feeding behaviour of the poecilostomatoid copepods *Oncaea* spp. On chaetognaths. *J. Marine Systems*, **15**, 475-482 (1998). (with Y-H, Go and B-C, Oh).

23) Life history, distribution, seasonal variability and feeding of pelagic chaetognath *Sagitta elegans* in the Subarctic Pacific: Areview. *Plankton Biol. Ecol.*: **45**, 1-17 (1998).

24) Springtime abundance of Chaetognaths in the shelf region of the northern Gulf of Alaska, with observations on the vertical distribution and feeding of *Sagitta elegans*. *Fish. Oceanogr.* **8**, 93-103 (1999). (with R. D. Brodeur)

25) Mass occurrence of bathypelagic chaetognath

Eukrohnia fowleri from the Arabian Sea and Bay of Bengal. *Indian J. Mar. Sci.* **28**, 163-168 (1999).

26) Feeding of carnivous zooplankton, chaetognath in the Pacific, *In: Dynamics and Characterization of Marine Organic Matter*. Tanoue, E. and T. Hama (editor), TERAPUB, Tokyo, 257-276 (2000).

4. 2001年7月23日(月) 東京水産大学において幹事会(第2回)が開催された。主な議事は下記のとおり。

- (1) 報告事項
1. 本年度の日仏会館シンポジウムとして「気候と地球の水」が開催される。開催予定日は12月1日(土)または12月15日(土)に予定されている。
 2. 平成13年6月26日(火)に日仏会館において、日仏関連諸学会協議会が開催され、本学会からは森永幹事と佐伯会員が出席した。理系諸学会合同シンポジウムの開催および会館のvisibilityをあげることについて協議された。
 3. 学会誌La merの編集状況が報告された。
 4. その他。
- (2) 審議事項
1. 日仏海洋学会論文賞の規定について、他学会の例をもとに論議された。次回幹事会までに庶務幹事を中心に原案を作成することとした。
 2. 水産学会記念創立70周年国際シンポジウム時に展示する、学会の概要照会のパネルについて検討し、今後さらに検討を続けることとした。
 3. 学会のホームページを開設することについて、記載内容を含め今後検討することとした。平成13年度学術研究発表会、総会の日程を5月27日(日)に決定した。
 4. 研究発表申込期間は4月2日~5月2日とし、本年度より講演要旨集を作成することとした。

5. 新入会員(正会員・学生会員*)

氏名	所属・住所等	紹介者
大森 保	〒903-0807 沖縄県那覇市首由久場川町1-112-13	山口征矢
橋詰和慶*	東京大学海洋研究所海洋科学国際センター 〒164-8639 中野区南台1-15-1	寺崎 誠

6. 所属・住所等変更(受付順)

高橋 暁	産業技術総合研究所(名称変更)
渡辺 武	〒228-0802 相模原市上鶴間6-10-38 コーポクレイン東林間206号
長谷川一幸	日本大学生産工学研究科土木工学専攻 〒275-8575 習志野市泉野1-2-1

7. 退会 (逝去退会)

丸茂 隆三, 黒沼 勝造, 糸刈 長敬

8. 受贈図書 (受付順)

国立情報学研究所ニュース 4, 5

神戸海洋気象台 報 219

RESTEC 47

高知大学海洋生物教育研究センター研究報告

Bullrtin of Marine Science and Fisheries 20

神奈川県立博物館研究報告 30

なつしま 184, 185, 186, 187, 188

農業工学関係研究成果情報 (H12年度)

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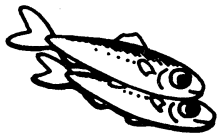
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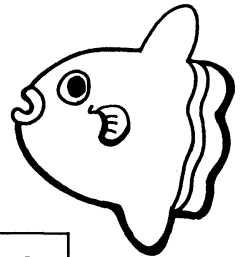
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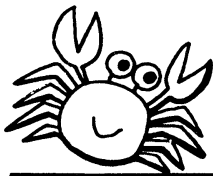


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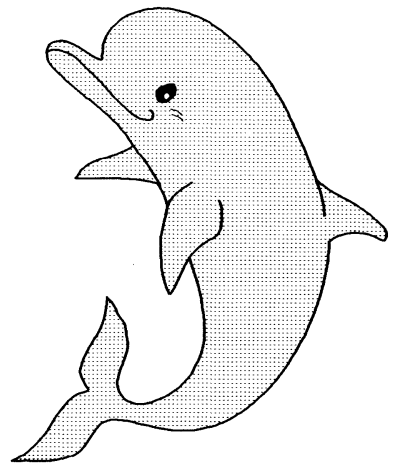
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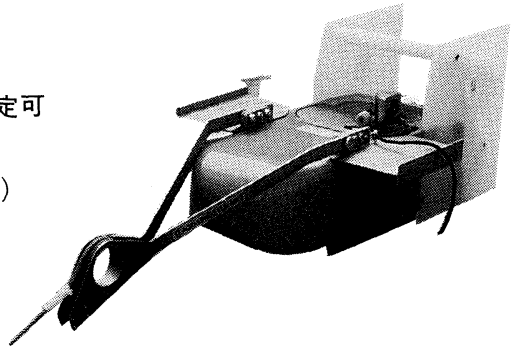
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