



Benchmark of plankton images classification: emphasizing features extraction over classifier complexity

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Abstract. Plankton imaging devices produce vast datasets, the processing of which can be largely accelerated through machine learning. This is a challenging task due to the diversity of plankton, the prevalence of non-biological classes, and

- 15 the rarity of many classes. Most existing studies rely on small, unpublished datasets that often lack realism in size, class diversity and proportions. We therefore also lack a systematic, realistic benchmark of plankton image classification approaches. To address this gap, we leverage both existing and newly published, large, and realistic plankton imaging datasets from widely used instruments. We evaluate different classification approaches: a classical Random Forest classifier applied to handcrafted features, various Convolutional Neural Networks (CNN), and a combination of both. This work aims
- 20 to provide reference datasets, baseline results, and insights to guide future endeavors in plankton image classification. Overall, CNN outperformed the classical approach but only significantly for uncommon classes. Larger CNN, which should provide richer features, did not perform better than small ones; and features of small ones could even be further compressed without affecting classification performance. Finally, we highlight that the nature of the classifier is of little importance compared to the content of the features. Our findings suggest that small CNNs are sufficient to extract relevant information
- 25 to classify small grayscale plankton images. This has consequences for operational classification models, which can afford to be small and quick. On the other hand, this opens the possibility for further development of the imaging systems to provide larger and richer images.

1 Introduction

Plankton, defined as organisms unable to swim against currents, are crucial components of oceanic systems as they form the
basis of food webs and contribute to organic carbon sequestration (Ware and Thomson 2005; Falkowski 2012). They have
been the subject of scientific research for centuries (Péron and Lesueur 1810). The definition of planktonic organisms, based
on motility and ecological niche rather than phylogeny, means that it encompasses a wide range of taxonomic clades



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(Tappan and Loeblich 1973). Furthermore, within these clades, plankton is known to be particularly diverse (Hutchinson 1961). Thus, planktonic organisms cover a wide range of size (from a few micrometers to several meters), shape, opacity, color, etc. While some planktonic taxa are ubiquitous (e.g. copepods), many are rare and sparsely distributed (e.g. fish larvae, scyphomedusae) (Ser-Giacomi et al. 2018).

Historically, plankton was studied by sampling with nets and pumps followed by identification and counting by taxonomists. These approaches, still used today, are precise but time-demanding. Quantitative imaging and automated identification are 40 now complementing traditional methods of plankton observation, with various imaging instruments developed to generate quantitative data (Lombard et al. 2019). Some of these instruments image collected samples, such as the ZooScan (Gorsky et al. 2010), the FlowCAM (Sieracki et al. 1998), or the ZooCAM (Colas et al. 2018). Others acquire images in situ, such as the Underwater Vision Profiler (UVP; Picheral et al. 2010, 2021), the In Situ Ichthyoplankton Imaging System (ISIIS; Cowen and Guigand 2008), the Imaging FlowCytobot (IFCB; Olson and Sosik 2007), or the ZooGlider (Ohman et al. 2019). These instruments vary significantly in terms of targeted size range, imaging technique, and deployment requirements, each 45 necessitating distinct processing pipelines. Moreover, the growing availability and ease of use of these instruments are generating an ever-increasing volume of plankton imaging data. Most of this data is now processed through automated algorithms. Among the various processing tasks, detecting or identifying organisms is commonly performed using supervised machine learning, where an algorithm learns patterns from training data and then generalizes these patterns to new data. However, the software pipelines have not progressed as fast as the hardware in many cases, causing a bottleneck in 50 data processing (Malde et al. 2020).

Automated classification of plankton images is a challenging computer science task. To begin with, planktonic communities, and therefore the resulting image datasets, exhibit significant class imbalance. In other words, a few classes contribute to a

- 55 substantial part of the dataset, while others classes are poorly represented. This specificity of plankton image datasets contrasts with standard benchmark image datasets where classes are almost evenly distributed: between 732 and 1300 images for each of the 1000 classes in ImageNet (Russakovsky et al. 2015). As a consequence, rare planktonic classes are harder to predict for automated algorithms (Lee et al. 2016; Van Horn and Perona 2017; Schröder et al. 2019). Secondly, planktonic organisms encompass a wide range of taxa and form a morphologically heterogeneous group, varying in size,
- 60 shape and opacity. More specifically, certain classes can exhibit significant intraclass variation: for instance, when morphological differences arise from life stages (e.g., doliolids) or when a class includes diverse, but rare, objects grouped together, as they are too uncommon to warrant separate classes (e.g., fish larvae). This variability can lead to confusion between classes (Grosjean et al. 2004). In addition to diverse classes of living organisms, real-world plankton image datasets comprise a considerable amount of non-living objects, such as marine snow aggregates or bubbles (Benfield et al. 2007);
- 65 these classes often constitute the majority of the datasets (Ellen et al. 2019; Schröder et al. 2019; Irisson et al. 2022). Finally, plankton images collected by quantitative instruments are typically low in resolution (with edges measuring only a few





hundred pixels or less) and are often grayscale or with little variation in color; therefore the distinction among classes needs to be made from a relatively small amount of information.

- 70 Historically, the automatic classification of plankton images involved training machine learning classifiers using handcrafted features extracted from the images. These manually extracted features, representative of the morphology of the objects to classify, aim to summarize the image content in numerical form, providing a concise representation that facilitates the classification process. Typical handcrafted features were global image moments (size, average gray, etc.; Tang et al. 1998), texture features such as gray-level co-occurrence matrices (Hu and Davis 2005), or shape features from Fourier transforms of
- 75 the contour (Tang et al 1998). Classifiers included Support Vector Machines (SVM; Luo et al. 2004; Hu and Davis 2005; Sosik and Olson 2007), Random Forests (RF; Gorsky et al. 2010) or Multi-Layer Perceptrons (MLP; Culverhouse et al. 1996). Several studies compared various classifiers trained on a common set of features, revealing varying results depending on the dataset, but ultimately no significant difference in their performance (Grosjean et al. 2004; Blaschko et al. 2005; Gorsky et al. 2010; Ellen et al. 2015, 2019). This suggests that the performance of classical approaches is not driven by the
- 80 classifier as much as by the number and diversity of features that are fed to it. Indeed, classification performance usually increases with a richer set of features (Blaschko et al. 2005). Nevertheless, this may not be true if some features are redundant or introduce noise into the data, hence the importance of feature selection (Sosik and Olson 2007; Guo et al. 2021). It also means that no universal set of features can be produced to identify all plankton traits across instruments, and the optimal set of features is therefore instrument and dataset dependent (Orenstein et al. 2022). Creating this optimal set of
- 85 features is a challenging task, as it requires both expertise in biology (to know what to extract) and in computer science (to know how to do it); feature engineering has therefore emerged as a complete research field (Guyon and Elisseeff 2003). In the following, we will refer to these two-step methods (1 handcrafted feature extraction and 2 classification) as "classic approaches", in contrast to the "deep approaches" introduced later.
- 90 Among classifiers, RF is a tree-based ensemble learning method that has shown high accuracy and versatility among computer vision tasks (Hastie et al. 2009). Each decision tree in the "forest" is trained on a random subset of the data (i.e. bootstrap), and at each step, it considers a random selection of predictors (or features) to split the data according to labeled classes. The tree keeps splitting until it reaches a stopping point, such as a maximum number of splits. During prediction, each object passes through the tree until it reaches a terminal leaf, where it is classified based on the majority class within
- 95 that leaf. By averaging the results from multiple trees, RF reduces the risk of overfitting (Breiman 2001). Fernández-Delgado et al. 2014, who evaluated the performances of nearly 180 classifiers on various datasets, concluded that RF outperformed all others. Gorsky et al. 2010 previously reached this conclusion on a ZooScan images dataset, resulting in a widespread use of RF classifiers later on. The IFCB data processing pipeline also switched from SVM to RF (Anglès et al. 2015). Finally, EcoTaxa (Picheral et al. 2017), a web application dedicated to the taxonomic annotation of images, initially implemented a
- 100 RF classifier to classify unlabeled images.



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However, since 2015, an increasing proportion of plankton image classification studies have employed deep learning methods, especially Convolutional Neural Networks (CNN). CNN are a kind of artificial neural network, typically used for pattern recognition tasks like image segmentation or classification. Their architecture is inspired from the visual cortex of animals, where each neuron reacts to stimuli from a restricted region (Dyck et al. 2021). In the case of an image classification task, a CNN directly takes an image as input (as opposed to classic approaches for which image features need to be extracted first), transforms it in various ways (the "Convolutional" part), combines the resulting features as input for a set of interconnected "neurons" that further reduce the information (the "Neural Network" part), and finally outputs a probability for the image to belong to each class; the class of highest probability is chosen as the predicted label. In contrast to classical approaches described above, the classification task with CNN is performed in a single step, where the feature 110 extractor and the classifier are trained simultaneously. This process optimizes the deep features specifically for the classification task. Moreover, those features can be used to train any kind of classifier, often resulting in better classification

CNN, first developed in 1990 (LeCun et al. 1990) and popularized in 2012 (Krizhevsky et al. 2012), were applied to 115 plankton image classification for the first time in 2015, during a challenge hosted on the online platform Kaggle¹. Since then, numerous studies have demonstrated the effectiveness of CNN in recognising plankton images (Dai et al. 2016; Lee et al. 2016; Luo et al. 2018; Cheng et al. 2019; Ellen et al. 2019; Lumini and Nanni 2019; Schmid et al. 2020). On a few plankton images datasets, CNN have proven to reach higher prediction accuracy than the classical approach of handcrafted features

performance than with handcrafted features (Orenstein and Beijbom 2017).

- 120 extraction followed by classification (Orenstein et al. 2015; Kyathanahally et al. 2021; Irisson et al. 2022). Currently, research on the classification of plankton images, or images of any other type of marine organisms, is dominated by CNN (Irisson et al. 2022; Rubbens et al. 2023). While CNN remain a dominant method for image classification, they have been surpassed by vision transformers (Vaswani et al. 2017), a newer state-of-the-art approach. However, vision transformers are less data-efficient than CNN, requiring larger datasets and greater computational resources for effective training (Raghu et
- 125 al. 2021). When applied to plankton image classification, vision transformers have shown only marginal improvements over CNN (Kyathanahally et al. 2022; Maracani et al. 2023).

A relatively recent review (Irisson et al. 2022) revealed that over 175 papers have addressed the topic of automated classification of plankton images. As shown earlier, a few compared classifiers explicitly, with varying outcomes. But overall, these 100+ studies used different datasets, often only one per study, and most of which were not publicly released. The datasets varied in terms of number of classes and number of images, two factors that significantly affect performance.

They also reported different performance metrics and the one most commonly reported (global accuracy) is unrepresentative

¹ https://www.kaggle.com/c/datasciencebowl/



for unbalanced datasets (Soda 2011). Indeed, out of the 10 most cited papers in the field (Irisson et al. 2022), 8 conducted a plankton classification experiment, but only 4 reported per class metrics or a confusion matrix (others only report global metrics such as accuracy). A similar pattern is observed among the papers cited here: of the 33 papers that performed a plankton classification task, only half reported metrics beyond global metrics (Table S1). Looking at the bigger picture, it appears that performance has remained relatively stable over time, while the taxonomic classification tasks became increasingly difficult since, with richer and larger datasets, more taxa were labeled (Irisson et al. 2022). This suggests that classifiers improved. However, this is unquantifiable, for all the reasons above. Nonetheless, three major plankton image datasets have been published and used in several studies (Table 1), while a few other studies have focused on smaller versions of these datasets (Dai et al. 2016; Zheng et al. 2017; Lumini and Nanni 2019). These benchmark datasets share several important characteristics: they are large (though this is debatable for PlanktonSet 1.0), representative of true data (with minimal alteration of class distribution and inclusion of all classes, such as detritus or miscellaneous), and accessible online. This highlights that a move towards standardization and intercompatibility is ongoing.

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Nama	Doforoncos	Imaging	Composition		D elevent publications	
Name	Kelei ences	instrument	Images	Classes	- Relevant publications	
WHOI-plankton	Orenstein et al. 2015; Sosik, Peacock, and Brownlee 2015	IFCB	3.5 M	103	Lee et al. 2016; Dai et al. 2017; Orenstein and Beijbom 2017; Cui et al. 2018; Kyathanahally et al. 2021, 2022; Maracani et al. 2023	
ZooScanNet	Elineau et al. 2024	ZooScan	1.4 M	93	Malde and Kim 2019; Schröder et al. 2019; Kyathanahally et al. 2021, 2022; Maracani et al. 2023	
PlanktonSet 1.0	Cowen et al. 2015	ISIIS	30,336	121	Dieleman et al. 2016; Py et al. 2016; Rodrigues et al. 2018; Uchida et al. 2018; Kyathanahally et al. 2021, 2022; Maracani et al. 2023	

 Table 1: Common plankton images benchmark datasets.

Currently, despite several years of active research on the topic and while CNN have been applied to plankton images for more than five years (Luo et al. 2018), a systematic, global comparison of classifier performance is still lacking. Leveraging





both previously published and new published plankton imaging datasets, the motivation for this study is to provide such a systematic, operational benchmark that evaluates practical and accessible approaches suitable for real-world applications. This includes starting with a classical feature-based image classification approach and exploring a few deep-learning methods. All are applied on large, realistic, and publicly released datasets from six commonly used plankton imaging 155 instruments, to encompass some of the variability in imaging modalities, processing pipelines, and target size ranges present in plankton imaging. For the classical approach, we use the handcrafted features natively extracted by the software

- associated with the instrument, assuming that they were engineered to be relevant for those images, and a RF classifier, given its popularity and performance on plankton images. For the deep approach, our base model is a relatively small and easy to train CNN (MobileNet V2), readily accessible to non ML specialists and below state of the art hardware. In addition
- 160 to this benchmark, we perform additional comparisons to tackle the following questions: (i) In which conditions do CNN strongly improve classification performance over the classical approach? (ii) Is per-class weighting of errors effective to counter the effect of class imbalance in plankton datasets? (iii) How rich do features need to be for plankton images classification: are larger CNN needed or, on the contrary, can features be compressed? (iv) What are the relative effect of features (deep vs. handcrafted) and classifier (MLP vs. RF) on classification performance?

165 2 Material and method

2.1 Datasets

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2.1.1 Imaging tools

We used datasets from six widely used plankton imaging instruments, each with distinct properties such as deployment methods or the size range of targeted organisms (Table 2). For a detailed review of these instruments, refer to Lombard et al. 2019.

Instrument	Deployment	Covered size range	Reference
FlowCAM	Ex situ (laboratory, ship)	20 to 200 µm	(Sieracki et al. 1998)
IFCB	In situ (mooring)	10 to 100 µm	(Olson and Sosik 2007) 175
ISIIS	In situ (ship-towed)	< 1 mm to several cm	(Cowen and Guigand 2008)
UVP6	In situ (CTD rosette, mooring, AUV)	$620 \ \mu m$ to a few cm	(Picheral et al. 2021)
ZooCAM	Ex situ (laboratory, ship)	> 300 µm	(Colas et al. 2018)
ZooScan	Ex situ (laboratory)	200 μm to a few cm	(Gorsky et al. 2010)

Table 2: Main characteristics of the plankton imaging instruments used to collect the datasets.



180 2.1.2 Image processing

Each imaging tool had its own specific image processing and feature extraction pipeline. The motivation here is to use these tools "out of the box", as other plankton ecologists would. ISIIS data was processed using Apeep (Panaïotis et al. 2022), and features were extracted using Scikit-image (Walt et al. 2014). The IFCB data processing relied on several MATLAB scripts (Sosik and Olson 2007) to segment objects and extract different types of features. The UVPapp application (Picheral et al.

185 2021) was developed to process UVP6 images and extract features. Both ZooScan and FlowCAM data were processed using ZooProcess (Gorsky et al. 2010), which generates crops of individual objects together with a set of features, extracted by ImageJ (Schneider et al. 2012). The processing of ZooCam data was very similar to the processing of ZooScan and FlowCAM data (Colas et al. 2018). Thus, for all datasets, each grayscale image was associated with a set of handcrafted features, which depended on the instrument but were mostly global features, related to shape and gray-levels, and a label.

190 2.1.3 Datasets assembling and composition

All datasets were generated in a similar way: complete, real-world datasets were sorted by human operators; All classifications were reviewed by one independant operator for each dataset. Except for IFCB and ZooCAM, samples particularly rich in some rare classes were added to the dataset (all images, not just those of the class of interest). Classes still containing fewer than ~100 objects were merged into a taxonomically and/or morphologically neighboring class. If no

- 195 relevant merging class could be found, objects were assigned to a miscellaneous class together with objects impossible to classify. Therefore, every single object from the original samples was included in the classification task, ensuring that the metrics computed on these datasets were as relevant to a real-world situation as possible. The IFCB images were taken from Sosik et al. 2015 (years 2011-2014); the images for other instruments were taken from EcoTaxa (Picheral et al. 2017), with the permission of their owners. Full references for each dataset are provided in Table 3. The number of images in the 200 resulting datasets ranged from 301,247 to 1,592,196, in 32 to 120 classes (Table 3). As expected, the datasets collected in
- situ (ISIIS, UVP6, and IFCB) were particularly rich in marine snow and other non-living objects, resulting in a low proportion of plankton.

To assess performance at a coarser taxonomic level, which may be sufficient in some applications and is more comparable to 205 older papers tackling automated classification of plankton images (e.g. Culverhouse et al. 1996; Sosik and Olson 2007; Gorsky et al. 2010), each class was assigned to a broader group (Tables 4, S2-S6). Each class/group was then categorized as planktonic or non-planktonic (i.e. detritus and imaging artifacts), allowing metrics to be computed for planktonic organisms only, excluding the, sometimes dominant, non-living objects (Table 3). The datasets were split, per class, into 70% for training, 15% for validation and 15% for testing, once, before all experiments. This split ensured that the majority of the data



210 was used for training, maximizing model learning, while preserving a sufficient portion for validation and testing (at least 10 objects for the rarest classes in FlowCAM and ISIIS datasets).

Table 3: References and dataset composition in terms of the numbers of images, classes and handcrafted features, as well a	as the
proportion of plankton (i.e. living organisms, as opposed to detritus and imaging artifacts).	

Instrument	Dataset reference	Composition					
mstrument		<pre># images [min; max per class]</pre>	Classes	Features	% plankton		
FlowCAM	(Jalabert et al. 2024)	301,247 [74 ; 69,085]	93	47	36.2		
ISIIS	(Panaïotis et al. 2024)	408,166 [70 ; 321,335]	32	31	15.3		
UVP6	(Picheral et al. 2024)	634,459 [87 ; 508,817]	54	62	7.7		
ZooCAM	(Romagnan et al. 2024)	1,286,590 [81 ; 204,132]	93	48	67.8		
ZooScan	(Elineau et al. 2024)	1,451,745 [90 ; 241,731]	120	48	71.2		
IFCB	(Sosik et al. 2015)	1,592,196 [90 ; 1,177,499]	69	72	12.6		

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2.2 Classification models

Each dataset was classified using different models, described below. The training procedure was the same for all models and datasets: (i) models were fitted to the training split, according to a loss metric, (ii) hyperparameters were assessed based on the same loss metric but computed on the independent validation split to limit overfitting, (iii) the model with optimal hyperparameters was used to predict the never-seen-before test split, only once, and various performance metrics were

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computed.

The RF classifiers were implemented using Scikit-learn (Pedregosa et al. 2011). The CNN models were implemented using Tensorflow (Abadi et al. 2016). Training and evaluation were performed on two Linux machines, depending on the model: a
Dell server equipped with a Quadro RTX 8000 GPU and a node of the Jean-Zay supercomputer, equipped with a V100 SXM2 GPU.

The code to reproduce all results is available at https://doi.org/10.5281/zenodo.14261492 (Panaïotis and Amblard 2025).



2.2.1 Classic approach

230 A RF classifier was trained on handcrafted features extracted from images by the software dedicated to each instrument. Their number ranged from 31 to 72 depending on the software (Table 3). Most features were global features, computed on the whole object: morphological features were computed on the object silhouette; gray-levels features were summaries of the distribution of gray levels in the object. In the case of IFCB, additional texture features were extracted, in the form of gray level co-occurrence matrices. The diversity of features is known to be crucial for the performance of the classifiers (Blaschko 235 et al. 2005).

The loss metric used during training and validation was categorical cross-entropy, which optimizes the model's confidence in predicting the correct class by minimizing the difference between predicted probabilities and actual labels. While this helps improve accuracy, it does not directly optimize for accuracy itself, which is based solely on whether predictions are correct, not on the confidence of those predictions. In terms of hyperparameters, the number of features used to compute each split was set to the square root of the number of features (which is the default for a classification task, Hastie et al. 2009) and the minimum number of samples in a terminal node was set to 5. The optimal number of trees was investigated using a grid

search procedure, over the values 100, 200, 350, and 500; for each, the classifier was fitted on the training split and evaluated on the validation split. The number of trees leading to the lowest validation loss was selected. This classic approach is 245 illustrated in the first row of Fig. 1.

2.2.2 Convolutional neural network

Since our goal here is to assess the performance of easy-to-use, turnkey models that most research teams should be able to deploy, we chose a rather small CNN (MobileNet V2; Sandler et al. 2019), as our reference model. In addition, we also evaluated the performance of much larger CNN: EfficientNet V2 (Tan and Le 2021), in its S and XL versions.

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Images were resized and padded to match the input dimensions required by each CNN model (MobileNet V2: 224×224×3; EfficientNet V2 S: 384×384×3; EfficientNet V2 XL: 512×512×3). Since each image was originally single-channel, the single channel was replicated across the typical three color channels used in CNN. To preserve aspect ratio, each image was resized so that its longest side equaled the model's input size, then padded to a square format using the median value of the

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border pixels to maintain a homogeneous background (Orenstein et al. 2015; Ellen et al. 2019). Finally, the grayscale channel was replicated to create three identical channels and achieve the desired shape. Since training a CNN from scratch is time and data-consuming, we applied transfer learning by using a feature extractor pre-trained on the ImageNet dataset. The pre-trained feature extractor could be used as it is, as the features extracted by a model trained on generic datasets have also proven to be relevant for other tasks (Yosinski et al. 2014), such as plankton classification (Orenstein and Beijbom 2017;



260 Rodrigues et al. 2018; Kyathanahally et al. 2021). But they can also be fine-tuned on the target dataset to achieve better performance (Yosinski et al. 2014), which is what we did here, for each dataset.

In a CNN, the typical classifier following the feature extractor is a MLP. To prevent overfitting, we added a dropout layer (rate = 0.5) immediately after the feature vector, preventing the model from relying on a few key neurons only (Srivastava et

- al. 2014) This was followed by a fully connected layer with either 600 or 50, depending on the model, to explore how the layer size impacts performance. Finally, the model ended with a classification head, the size of which depended on the number of classes to predict. This resulted in 4.5 M parameters for the smaller CNN and 208 M for the larger one. All models are described in Fig. 1.
- 270 Data augmentation (Shorten and Khoshgoftaar 2019) was used to improve model generalization ability and performance, especially for rare classes. Images from the training set were randomly flipped vertically and horizontally, zoomed in and out (up to 20%), and sheared (up to 15°). Such a process increases the diversity of examples seen during training, improving generalization ability of the model (Dai et al. 2016). Images were not rotated because objects from a few classes had a specific orientation (e.g. vertical lines in the ISIIS dataset, or some organisms that have a specific orientation in datasets
- 275 collected in situ). As for the RF, the loss metric was the categorical cross entropy. At the end of each training epoch (i.e. a complete run over all images in the training split), both loss and accuracy were computed on the validation split, to check for overfitting, and model parameters were saved.

The feature extractor, fully connected and classification layers were trained for 10 epochs (5 epochs for EfficientNets). 280 Monitoring the loss on the validation set revealed that this was sufficient for exhaustive training. The optimizer used the Adam algorithm, with a decaying learning rate from an initial value of 0.0005 and a decay rate of 0.97 per epoch. Similarly to the optimization of the number of trees of the RF models, the number of training epochs was optimized by retaining the parameters associated with the epoch presenting the minimum validation loss, hence reducing overfitting (Smith 2018).

2.2.3 Hybrid approaches

Finally, to discriminate the effect of the feature extractor (either handcrafted or deep) and the classifier (either a RF or a MLP), the deep features produced by the fine-tuned MobileNet V2 (n = 1792) were used to train a RF classifier. Furthermore, to compare RF trained on similar numbers of features and to evaluate the importance of feature richness, we reduce the dimension of those deep features from 1792 to 50 using a principal component analysis (PCA) fitted on the training set only, before feeding them into the RF classifier. These two "hybrid" approaches are illustrated in the last two rows of Fig. 1.



2.2.4 Class weights

In an unbalanced dataset, well-represented classes are given more importance because examples from these classes are more frequent in the loss calculation, while very small classes are almost negligible. As a result, performance on these small classes is often very poor (Luo et al. 2018; Schröder et al. 2019). To address this imbalance, training data can be resampled to achieve a more balanced distribution (e.g. oversampling poorly represented classes and/or undersampling dominant classes), a set of methods known as dataset-level approaches (Sun et al. 2009). Alternatively, the classifier can be tuned so that the misclassification cost is higher for small classes (i.e. algorithm-level approaches). Although both types of methods were shown to improve classification performance (at least for a binary classification task, McCarthy et al. 2005), altering the distribution of the training data may generate poor results when predicting new data with a different distribution

300 (Moreno-Torres et al. 2012; González et al. 2017). Thus, a class-weighted loss was implemented to increase the cost of misclassifying rare plankton classes. Class weights can be set as the inverse frequency of classes, or smoother alternative such as root or fourth-root of the inverse frequency (Cui et al. 2019), which gives, for class *i*:

$$w_i = \left(\frac{\max\left(c\right)}{c_i}\right)^{0.25}$$

The effect of these per-class weights was investigated by training both weighted and non-weighted versions of a RF on native features and of the reference CNN (Mob + MLP_{600} ; Fig. 1).







Figure 1: Description of the models tested. Each model consists of a feature extractor and a classifier, and is named accordingly. For each model, the brown line represents the feature vector and its length is indicated. For MLPs, the number in subscript gives the size of the fully connected layer. RF = Random Forest, MLP = Multilayer Perceptron, NW = no weights (i.e. learning not weighted by class size), PCA = Principal Component Analysis. The colors defined here are consistent with other figures. The

MobileNet V2 with a fully connected layer of size 600 (Mob + MLP₆₀₀, in dark blue) will be considered as a reference model and

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repeated in all figures.



2.2.5 Model evaluation

- 315 After each model in Fig. 1 was trained and tuned for either the number of trees (for classical models) or the number of epochs (for CNN) on each dataset, models were evaluated on the test split, to which they had not been previously exposed. Usual metrics were computed: accuracy score (percentage of objects correctly classified), balanced accuracy, class-wise precision (percentage correct in the predicted class) and recall (percentage correct within the true class).
- 320 In datasets with strong class imbalance such as many plankton datasets accuracy alone can be misleading. For instance, in a highly unbalanced dataset where 99% of objects belong to a single class, a model that classifies every object into that class would be completely uninformative but would still achieve an accuracy of 99%. Similarly, in an 11-class dataset with one dominant class comprising 90% of the data (and each of the other classes making up only 1%), a classifier that randomly assigns classes according to these proportions would still yield an accuracy of approximately 81%, despite offering little real predictive value. Therefore, to better gauge the quality of our models on unbalanced datasets, the same performance metrics
- were also computed on the output of such a random classifier. In addition, the balanced accuracy score, computed as the simple average of per-class recall scores, was also computed, as it is a better estimate of model performance in such a scenario (Kelleher et al. 2020).
- Furthermore, in the case of plankton datasets, the dominant classes are often not plankton (detritus, mix, etc.). The accuracy value is mostly driven by these classes (Orenstein et al. 2015) and, therefore, does not provide any information about the performance on plankton classes, which are often the subject of study. To focus on these classes, we also computed the average of precision and recall per class, weighted by the number of objects in the class, but using only plankton classes. Averaged plankton recall gives a direct indication of the proportion of planktonic organisms that were correctly predicted.
 Averaged plankton precision gives an indication of how "pure" the predicted plankton classes are.

3 Results

3.1 Training time

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Training and evaluation times were always shorter for the classical approach (using pre-extracted handcrafted features and a RF classifier) than for CNN (which combined feature extraction and classification). Running on 12 CPU cores, gridsearch, training, and evaluation for the RF classifier based on native features took less than an hour for the smallest dataset (ISIIS, ~400,000 objects) and a few hours for the IFCB dataset (~1.6 M objects). The extraction of handcrafted features could not be reliably timed, as it is performed using very different software, but is usually in the order of hours for about a million objects. In contrast, it took 5h to train the MobileNet V2 + MLP₆₀₀ for 10 epochs on the ISIIS dataset but 15h for the same number of epochs on the IFCB dataset, using a Quadro RTX 8000 GPU.



345 3.2 Benchmark performance of MobileNetV2, our reference model

On the six large and realistic plankton image datasets included in this study, a small CNN model (MobileNetV2) trained with per-class weights achieved strong performance while remaining easy to implement. The balanced accuracy across all classes ranged from 79% to 90%, with plankton class precision and recall reaching 80%, except for ISIIS and UVP6 datasets. These benchmark results are further compared to other approaches in the following sections.

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Table 4: Classification report for detailed classes in the ZooScan dataset. Reported values are F1-scores.

Class	Crownod	Not + DE	Mob +		Mob + PCA +
Class	Grouped	Nat + Kr	MLP600	EIIS + MLPOUU	RF
		Plankton			
Actinopterygii	Actinopterygii	23.8	87.9	91.6	94.5
egg <actinopterygii< td=""><td>Actinopterygii</td><td>35.3</td><td>88.3</td><td>88.3</td><td>90.5</td></actinopterygii<>	Actinopterygii	35.3	88.3	88.3	90.5
Neoceratium	Alveolata	0.0	92.3	89.5	92.7
Noctiluca	Alveolata	54.6	92.7	90.2	92.5
Amphipoda	Amphipoda	0.0	82.7	86.1	90.1
Cumacea	Amphipoda	30.4	91.2	94.0	94.8
Hyperiidea	Amphipoda	26.1	90.2	93.4	92.8
Annelida	Annelida	21.3	85.0	85.9	87.5
larvae <annelida< td=""><td>Annelida</td><td>0.0</td><td>72.9</td><td>75.2</td><td>75.0</td></annelida<>	Annelida	0.0	72.9	75.2	75.0
part <annelida< td=""><td>Annelida</td><td>35.7</td><td>86.2</td><td>85.4</td><td>88.2</td></annelida<>	Annelida	35.7	86.2	85.4	88.2
Tomopteridae	Annelida	7.0	92.1	91.8	89.6
Fritillariidae	Appendicularia	28.1	89.7	88.9	90.5
Oikopleuridae	Appendicularia	39.4	94.2	94.5	95.0
tail <appendicularia< td=""><td>Appendicularia</td><td>48.6</td><td>85.2</td><td>84.4</td><td>86.9</td></appendicularia<>	Appendicularia	48.6	85.2	84.4	86.9
trunk	Appendicularia	0.0	67.3	67.1	72.4
Chaetognatha	Chaetognatha	75.4	97.3	97.6	97.9
head <chaetognatha< td=""><td>Chaetognatha</td><td>0.0</td><td>56.9</td><td>69.8</td><td>72.4</td></chaetognatha<>	Chaetognatha	0.0	56.9	69.8	72.4
tail <chaetognatha< td=""><td>Chaetognatha</td><td>15.3</td><td>73.0</td><td>75.0</td><td>77.6</td></chaetognatha<>	Chaetognatha	15.3	73.0	75.0	77.6
cirrus	Cirripedia	9.1	68.5	59.5	68.6
cypris	Cirripedia	0.0	87.9	92.8	91.8
nauplii <cirripedia< td=""><td>Cirripedia</td><td>0.0</td><td>92.2</td><td>92.4</td><td>94.3</td></cirripedia<>	Cirripedia	0.0	92.2	92.4	94.3
Evadne	Cladocera	17.1	96.8	97.1	97.4
Penilia	Cladocera	39.9	96.8	97.0	97.7
Podon	Cladocera	0.0	88.3	87.8	87.6
Acartiidae	Copepoda	24.2	95.5	95.4	95.9



Calanidae	Copepoda	33.0	96.3	96.4	97.0
Calanoida	Copepoda	57.6	94.3	94.3	94.9
Calocalanus pavo	Copepoda	2.7	84.2	85.5	89.9
Candaciidae	Copepoda	11.9	95.5	95.1	95.5
Centropagidae	Copepoda	32.8	94.6	94.6	95.1
Copilia	Copepoda	0.0	88.5	94.2	95.1
Corycaeidae	Copepoda	28.5	96.3	96.6	97.2
Eucalanidae	Copepoda	16.8	88.4	90.2	91.3
Euchaetidae	Copepoda	21.3	94.2	94.1	96.2
Haloptilus	Copepoda	31.8	95.6	95.4	96.5
Harpacticoida	Copepoda	0.2	90.7	92.7	93.1
Heterorhabdidae	Copepoda	0.0	87.6	86.2	89.3
Metridinidae	Copepoda	14.7	94.6	94.6	95.7
Oithonidae	Copepoda	59.2	96.6	96.6	97.0
Oncaeidae	Copepoda	9.1	93.4	94.2	94.8
Pontellidae	Copepoda	54.8	97.0	96.5	98.6
Rhincalanidae	Copepoda	52.0	70.2	78.3	85.3
Sapphirinidae	Copepoda	0.0	91.8	91.2	91.9
Temoridae	Copepoda	23.4	96.0	96.0	96.9
Ctenophora	Ctenophora	0.0	67.0	72.3	81.1
cyphonaute	cyphonaute	29.8	98.4	98.5	98.4
larvae <luciferidae< td=""><td>Decapoda</td><td>16.4</td><td>95.2</td><td>95.4</td><td>97.9</td></luciferidae<>	Decapoda	16.4	95.2	95.4	97.9
larvae <porcellanidae< td=""><td>Decapoda</td><td>64.2</td><td>96.2</td><td>97.4</td><td>98.3</td></porcellanidae<>	Decapoda	64.2	96.2	97.4	98.3
megalopa	Decapoda	27.9	95.9	95.2	96.7
protozoea <penaeidae< td=""><td>Decapoda</td><td>0.0</td><td>84.2</td><td>87.6</td><td>92.3</td></penaeidae<>	Decapoda	0.0	84.2	87.6	92.3
protozoea <sergestidae< td=""><td>Decapoda</td><td>0.0</td><td>78.5</td><td>71.7</td><td>81.0</td></sergestidae<>	Decapoda	0.0	78.5	71.7	81.0
zoea <brachyura< td=""><td>Decapoda</td><td>40.0</td><td>95.7</td><td>96.7</td><td>97.5</td></brachyura<>	Decapoda	40.0	95.7	96.7	97.5
zoea <galatheidae< td=""><td>Decapoda</td><td>1.3</td><td>88.1</td><td>88.3</td><td>89.3</td></galatheidae<>	Decapoda	1.3	88.1	88.3	89.3
Doliolida	Doliolida	37.7	93.2	92.4	93.8
larvae <echinodermata< td=""><td>Echinodermata</td><td>0.0</td><td>80.6</td><td>76.6</td><td>84.0</td></echinodermata<>	Echinodermata	0.0	80.6	76.6	84.0
pluteus <echinoidea< td=""><td>Echinodermata</td><td>26.8</td><td>86.7</td><td>87.8</td><td>89.7</td></echinoidea<>	Echinodermata	26.8	86.7	87.8	89.7
pluteus <ophiuroidea< td=""><td>Echinodermata</td><td>13.4</td><td>91.0</td><td>92.5</td><td>92.0</td></ophiuroidea<>	Echinodermata	13.4	91.0	92.5	92.0
Eumalacostraca	Eumalacostraca	61.3	91.4	91.7	92.4
Eumalacostraca potentially protozoea	Eumalacostraca	26.1	83.0	81.4	83.8
larvae <mysida< td=""><td>Eumalacostraca</td><td>0.0</td><td>72.7</td><td>88.9</td><td>82.8</td></mysida<>	Eumalacostraca	0.0	72.7	88.9	82.8
Mysida	Eumalacostraca	76.5	86.4	91.6	94.4
Harosa	Harosa	1.6	76.7	75.1	74.2



Isopoda	Isopoda	67.1	98.8	97.6	98.2
Atlanta	Mollusca	0.0	84.8	83.9	90.9
Bivalvia <mollusca< td=""><td>Mollusca</td><td>12.6</td><td>95.0</td><td>95.5</td><td>95.8</td></mollusca<>	Mollusca	12.6	95.0	95.5	95.8
Cavolinia inflexa	Mollusca	58.2	97.5	96.2	97.2
Creseidae	Mollusca	47.4	93.7	94.0	94.2
Creseis acicula	Mollusca	67.6	94.5	94.4	94.9
Cymbulia peroni	Mollusca	0.0	80.0	72.7	76.5
egg <mollusca< td=""><td>Mollusca</td><td>1.5</td><td>76.7</td><td>77.0</td><td>75.7</td></mollusca<>	Mollusca	1.5	76.7	77.0	75.7
Gymnosomata	Mollusca	60.4	92.8	95.7	95.6
Limacinidae	Mollusca	25.3	96.1	96.3	96.9
part <mollusca< td=""><td>Mollusca</td><td>2.2</td><td>61.9</td><td>55.3</td><td>60.9</td></mollusca<>	Mollusca	2.2	61.9	55.3	60.9
Actiniaria	other_Cnidaria	16.7	93.0	93.3	89.8
ephyra	other_Cnidaria	36.7	86.4	91.5	91.3
Hydrozoa	other_Cnidaria	13.6	74.6	75.1	78.4
Obelia	other_Cnidaria	18.2	85.9	85.7	88.5
part <cnidaria< td=""><td>other_Cnidaria</td><td>0.0</td><td>14.8</td><td>44.0</td><td>44.6</td></cnidaria<>	other_Cnidaria	0.0	14.8	44.0	44.6
calyptopsis	other_Crustacea	12.2	93.5	94.3	93.3
larvae <stomatopoda< td=""><td>other_Crustacea</td><td>46.5</td><td>95.6</td><td>96.5</td><td>98.4</td></stomatopoda<>	other_Crustacea	46.5	95.6	96.5	98.4
metanauplii <crustacea< td=""><td>other_Crustacea</td><td>0.0</td><td>81.8</td><td>85.3</td><td>93.7</td></crustacea<>	other_Crustacea	0.0	81.8	85.3	93.7
nauplii <crustacea< td=""><td>other_Crustacea</td><td>4.6</td><td>91.5</td><td>91.8</td><td>93.3</td></crustacea<>	other_Crustacea	4.6	91.5	91.8	93.3
Ostracoda	other_Crustacea	46.4	96.4	96.7	97.6
part <crustacea< td=""><td>other_Crustacea</td><td>2.6</td><td>63.2</td><td>65.3</td><td>68.2</td></crustacea<>	other_Crustacea	2.6	63.2	65.3	68.2
Pyrosomatida	Pyrosomatida	22.2	93.9	95.4	94.8
Foraminifera	Rhizaria	25.7	89.7	89.8	90.4
Phaeodaria	Rhizaria	55.1	96.6	96.2	96.7
endostyle	Salpida	16.0	60.4	58.2	61.4
juvenile <salpida< td=""><td>Salpida</td><td>0.0</td><td>82.3</td><td>84.0</td><td>81.9</td></salpida<>	Salpida	0.0	82.3	84.0	81.9
nucleus	Salpida	11.5	68.6	71.4	74.7
Salpida	Salpida	42.1	92.9	92.3	93.4
Bassia	Siphonophorae	0.0	57.1	50.0	56.0
bract <abylopsis td="" tetragona<=""><td>Siphonophorae</td><td>34.9</td><td>91.2</td><td>89.0</td><td>89.9</td></abylopsis>	Siphonophorae	34.9	91.2	89.0	89.9
bract <diphyidae< td=""><td>Siphonophorae</td><td>12.0</td><td>85.9</td><td>86.0</td><td>87.9</td></diphyidae<>	Siphonophorae	12.0	85.9	86.0	87.9
eudoxie <abylopsis td="" tetragona<=""><td>Siphonophorae</td><td>0.0</td><td>90.3</td><td>92.1</td><td>89.6</td></abylopsis>	Siphonophorae	0.0	90.3	92.1	89.6
eudoxie <diphyidae< td=""><td>Siphonophorae</td><td>2.9</td><td>84.3</td><td>86.9</td><td>89.9</td></diphyidae<>	Siphonophorae	2.9	84.3	86.9	89.9
gonophore <abylopsis td="" tetragona<=""><td>Siphonophorae</td><td>12.1</td><td>90.9</td><td>90.2</td><td>93.5</td></abylopsis>	Siphonophorae	12.1	90.9	90.2	93.5
gonophore <diphyidae< td=""><td>Siphonophorae</td><td>30.0</td><td>93.2</td><td>93.4</td><td>94.2</td></diphyidae<>	Siphonophorae	30.0	93.2	93.4	94.2
nectophore <abylopsis td="" tetragona<=""><td>Siphonophorae</td><td>20.7</td><td>88.6</td><td>87.6</td><td>91.7</td></abylopsis>	Siphonophorae	20.7	88.6	87.6	91.7



nectophore <diphyidae< td=""><td>Siphonophorae</td><td>63.1</td><td>92.9</td><td>92.2</td><td>93.1</td><td></td></diphyidae<>	Siphonophorae	63.1	92.9	92.2	93.1	
nectophore <hippopodiidae< td=""><td>Siphonophorae</td><td>18.2</td><td>73.3</td><td>81.1</td><td>85.7</td><td></td></hippopodiidae<>	Siphonophorae	18.2	73.3	81.1	85.7	
nectophore <physonectae< td=""><td>Siphonophorae</td><td>59.5</td><td>87.4</td><td>81.8</td><td>84.7</td><td></td></physonectae<>	Siphonophorae	59.5	87.4	81.8	84.7	
part <siphonophorae< td=""><td>Siphonophorae</td><td>0.0</td><td>66.8</td><td>67.4</td><td>69.5</td><td></td></siphonophorae<>	Siphonophorae	0.0	66.8	67.4	69.5	
Physonectae	Siphonophorae	0.0	43.5	48.5	66.7	
siphonula	Siphonophorae	19.2	90.3	86.1	89.0	
Coscinodiscus	Stramenopiles	41.2	97.3	96.8	97.2	
actinula <solmundella bitentaculata<="" td=""><td>Trachylina</td><td>0.0</td><td>68.8</td><td>78.9</td><td>82.4</td><td></td></solmundella>	Trachylina	0.0	68.8	78.9	82.4	
Aglaura	Trachylina	57.9	91.8	91.7	93.0	
Liriope <geryoniidae< td=""><td>Trachylina</td><td>0.0</td><td>52.0</td><td>73.0</td><td>78.7</td><td></td></geryoniidae<>	Trachylina	0.0	52.0	73.0	78.7	
Rhopalonema velatum	Trachylina	49.1	85.6	85.2	87.2	
Solmundella bitentaculata	Trachylina	3.5	67.4	70.6	73.4	
	-					
average	-	22.9	85.5	86.6	88.5	
average		22.9 Non plankton	85.5	86.6	88.5	
average	artefact	22.9 Non plankton 76.7	85.5 80.8	<i>86.6</i> 80.0	88.5 79.8	
average artefact badfocus <artefact< td=""><td>artefact badfocus</td><td>22.9 Non plankton 76.7 19.6</td><td>85.5 80.8 63.1</td><td>86.6 80.0 62.9</td><td>88.5 79.8 63.1</td><td></td></artefact<>	artefact badfocus	22.9 Non plankton 76.7 19.6	85.5 80.8 63.1	86.6 80.0 62.9	88.5 79.8 63.1	
average artefact badfocus <artefact bubble</artefact 	artefact badfocus bubble	22.9 Non plankton 76.7 19.6 19.0	85.5 80.8 63.1 92.2	86.6 80.0 62.9 91.0	88.5 79.8 63.1 91.2	
average artefact badfocus <artefact bubble detritus</artefact 	artefact badfocus bubble detritus	22.9 Non plankton 76.7 19.6 19.0 55.2	85.5 80.8 63.1 92.2 82.9	86.6 80.0 62.9 91.0 81.4	88.5 79.8 63.1 91.2 81.6	
average artefact badfocus <artefact bubble detritus fiber<detritus< td=""><td>artefact badfocus bubble detritus fiber</td><td>22.9 Non plankton 76.7 19.6 19.0 55.2 62.9</td><td>85.5 80.8 63.1 92.2 82.9 74.6</td><td>86.6 80.0 62.9 91.0 81.4 74.7</td><td>88.5 79.8 63.1 91.2 81.6 74.8</td><td></td></detritus<></artefact 	artefact badfocus bubble detritus fiber	22.9 Non plankton 76.7 19.6 19.0 55.2 62.9	85.5 80.8 63.1 92.2 82.9 74.6	86.6 80.0 62.9 91.0 81.4 74.7	88.5 79.8 63.1 91.2 81.6 74.8	
average artefact badfocus <artefact bubble detritus fiber<detritus Insecta</detritus </artefact 	artefact badfocus bubble detritus fiber Insecta	22.9 Non plankton 76.7 19.6 19.0 55.2 62.9 27.1	85.5 80.8 63.1 92.2 82.9 74.6 84.3	86.6 80.0 62.9 91.0 81.4 74.7 86.9	88.5 79.8 63.1 91.2 81.6 74.8 89.6	
average artefact badfocus <artefact bubble detritus fiber<detritus Insecta egg<other< td=""><td>artefact badfocus bubble detritus fiber Insecta other_egg</td><td>22.9 Non plankton 76.7 19.6 19.0 55.2 62.9 27.1 59.7</td><td>85.5 80.8 63.1 92.2 82.9 74.6 84.3 92.2</td><td>86.6 80.0 62.9 91.0 81.4 74.7 86.9 91.0</td><td>88.5 79.8 63.1 91.2 81.6 74.8 89.6 92.4</td><td></td></other<></detritus </artefact 	artefact badfocus bubble detritus fiber Insecta other_egg	22.9 Non plankton 76.7 19.6 19.0 55.2 62.9 27.1 59.7	85.5 80.8 63.1 92.2 82.9 74.6 84.3 92.2	86.6 80.0 62.9 91.0 81.4 74.7 86.9 91.0	88.5 79.8 63.1 91.2 81.6 74.8 89.6 92.4	
average artefact badfocus <artefact bubble detritus fiber<detritus Insecta egg<other other<living< td=""><td>artefact badfocus bubble detritus fiber Insecta other_egg other_living</td><td>22.9 Non plankton 76.7 19.6 19.0 55.2 62.9 27.1 59.7 16.3</td><td>85.5 80.8 63.1 92.2 82.9 74.6 84.3 92.2 39.2</td><td>86.6 80.0 62.9 91.0 81.4 74.7 86.9 91.0 59.3</td><td>88.5 79.8 63.1 91.2 81.6 74.8 89.6 92.4 73.7</td><td></td></living<></other </detritus </artefact 	artefact badfocus bubble detritus fiber Insecta other_egg other_living	22.9 Non plankton 76.7 19.6 19.0 55.2 62.9 27.1 59.7 16.3	85.5 80.8 63.1 92.2 82.9 74.6 84.3 92.2 39.2	86.6 80.0 62.9 91.0 81.4 74.7 86.9 91.0 59.3	88.5 79.8 63.1 91.2 81.6 74.8 89.6 92.4 73.7	
artefact badfocus <artefact bubble detritus fiber<detritus Insecta egg<other other<living seaweed</living </other </detritus </artefact 	artefact badfocus bubble detritus fiber Insecta other_egg other_living seaweed	22.9 Non plankton 76.7 19.6 19.0 55.2 62.9 27.1 59.7 16.3 35.3	85.5 80.8 63.1 92.2 82.9 74.6 84.3 92.2 39.2 68.0	86.6 80.0 62.9 91.0 81.4 74.7 86.9 91.0 59.3 68.2	88.5 79.8 63.1 91.2 81.6 74.8 89.6 92.4 73.7 66.3	





3.3 Rare classes are where CNN outperform classical approaches

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Figure 2: Performance comparison between a small CNN (Mob + MLP600), a RF trained on handcrafted features and a random classifier on all six datasets. Both class weighted and non-weighted versions of the models were evaluated. The models are described in Fig. 1. Plain bars show the value of each metric at the finest taxonomic level, striped bars show the value after regrouping objects into broader ecological groups.

- 360 In terms of overall accuracy, the CNN performed only slightly better on all datasets than the classical approach of using handcrafted features and an RF classifier (+3.5% to +43.8% depending on the dataset; +15.1% on average) (Fig. 2). The use of class weights slightly decreased the accuracy of both the deep and classical approaches, as it focused training on small classes and less on large classes, which account for more in the computation of accuracy. Note that a random classifier achieved 55%, 61% and 63% accuracy on the detritus-dominated IFCB, ISIIS and UVP6 datasets, respectively. While the
- 365 accuracies of all non-random models were higher, they must be gauged in terms of the increase over the random model and not in absolute terms.

Deep approaches showed much higher balanced accuracies than classical ones, as well as improved precisions and recalls averaged over plankton classes; this was true both with and without weights (Fig. 2). The balanced accuracy of the random

370 classifier was very poor in all datasets, confirming that this metric is more relevant in datasets with many small classes. The improvements brought by CNN were associated with the fact that they performed better on non-dominant classes (e.g. Tables 4, S2-S6).



Class weights improved balanced accuracy for both deep (up to +8.2% for the UVP6 dataset) and classical approaches (up to +18.0% for the UVP6 dataset). Thus, as expected, giving more weight to small classes improved their learning by the classifier, but this was especially true for RF models. Weighting decreased plankton precision for both models, on all datasets: errors involving samples from large classes were less penalized, resulting in a greater contamination of plankton classes, i.e. lower precision. Symmetrically, the use of class weights improved the recall of plankton classes for all models (except MobileNet on the FlowCam dataset). Again, this improvement is expected since plankton classes, which typically contain fewer images than non-plankton ones (e.g. detritus), are given more weight, reducing the number of false negatives, i.e. increasing recall. Since applying class weights improved detection of underrepresented classes (primarily plankton), only the weighted versions of each model will be evaluated in the subsequent analysis.



3.4 Small CNN are sufficient for plankton image classification

385 Figure 3: Performance comparison between our reference CNN (Mob + MLP600), a CNN with a larger feature extractor (Eff S + MLP600 and Eff XL + MLP600) and a MobileNet followed by a smaller MLP (Mob + MLP50) on all six datasets. The models are described in Fig. 1. Plain bars show the value of each metric at the finest taxonomic level, striped bars show the value after regrouping objects into broader ecological groups.

Using a larger and supposedly richer feature extractor, such as EfficientNet S or EfficientNet XL, did not markedly improve performance metrics (Fig. 3). If anything, performance was lower with EfficientNet XL, likely due to immediate overfitting



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after the first epoch, causing the model to adhere too closely to the training data and impair its ability to generalize. This may be due to the relatively small training dataset, which, in proportion to the number of parameters in the model, increases the risk of overfitting. The effect was especially pronounced with the UVP6 dataset, which is not only small (~635,000 images) but also has a low proportion of plankton images (7.7%); both balanced accuracy and plankton-specific metrics (average precision and recall) were notably impacted. On the other hand, compressing the features before classification, by using a fully connected layer of size 50 instead of 600 after the MobileNet feature extractor, did not reduce classification performance (Fig. 3). Both results suggest that a relatively small model is enough to extract all informative content from the small, gravscale plankton images in these datasets.

small, grayscale plankton images in these datasets.



3.5 The features are more important than the classifier

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Figure 4: Performance comparison between our reference CNN (Mob + MLP600), a RF trained on deep features extracted by a MobileNet V2 without (Mob + RF) and with (Mob + PCA + RF) feature reduction, and a RF trained on handcrafted features on all six datasets. The models are described in Fig. 1. Plain bars show the value of each metric at the finest taxonomic level, striped bars show the value after regrouping objects into broader ecological groups.

405 Moving from native features to MobileNet deep features before the RF classifier significantly increased all classification metrics (Fig. 4). On the contrary, performance stayed the same when the MLP600 classifier was replaced by a RF after the same MobileNet feature extractor. This suggests that the classifier itself is of relatively little importance; rather, it is the



quality of the features that determines performance. Since features are optimized during CNN training, their quality aligns with the patterns the algorithm learns to improve classification accuracy.

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Finally, compressing features with a classification-agnostic dimension reduction method (PCA here) had very little effect on classification performance (Fig. 4). This supports the idea, stated in the previous section, that the information required to classify the relatively small, gray-scale plankton images captured by the instruments considered here can be efficiently summarized in only a few numbers (50 here). This opens operational possibilities since the feature extractor, the feature compressor and the classifier can be separated.

3.6 Performance on coarser groups



Figure 5: Density distribution (i.e. continuous histogram) of the difference in performance metrics per class when going from RF on native features to different deep models (colors), on the ZooScan datasets, at two taxonomic levels (rows).

420 Regrouping classes into broader ecological groups improved all performance metrics across all datasets and approaches (Fig. 2, 3, and 4), as it made the classification task easier. However, it is important to note that our method – regrouping classes after training on detailed classes – differs from retraining a model on grouped classes alone. In the latter approach, regrouping would increase the number of examples within each group, likely enhancing performance. Yet, this could also introduce more diversity within each class, sometimes referred to as "within-class subconcepts" (He and Garcia 2009),



- 425 which might reduce accuracy in certain, morphologically diverse, groups (e.g. both Appendicularia bodies and houses being labeled as Appendicularia). This decrease in performance is especially evident in miscellaneous classes containing objects that could not be assigned to other categories (Table 4, S2 - S6). The performance increase between detailed and coarse classes was larger for classical approaches, particularly on the ZooCam and ZooScan datasets (Fig. 2). This highlights the fact that classical approaches often confused fine-scale taxa, comprised within larger groups. A good example is Copepoda, which has 22 subclasses in the ZooCam dataset and 20 in the ZooScan dataset. The classification of some of these ~20
- classes was often poor with classical models while the classification of Copepoda, as a whole, was rather good. Since Copepoda represented a large percentage of the images in each dataset, 38% and 34% respectively, classifications metrics significantly improved when they were grouped.
- The other side of the same coin is that performance improvements when going from a RF on native features to different deep models were larger when the taxonomic level was more detailed. In Fig. 5, most classes show better performance with the deep models (to the right of zero), and the increase is more pronounced with detailed classes (top) than on regrouped ones (bottom), for precision in particular. In other words, deep models beat classical ones on almost all classes (most differences in per-class metrics were above zero) but, on datasets with more and smaller classes, CNN beat classical approaches more often and by a wider margin than on coarser datasets. This further supports that CNN are better than classical approaches specifically at classifying rare classes.

4 Discussion

4.1 Costs and benefits of using CNN

In terms of accuracy alone, CNN did not appear to offer a significant performance improvement over the classical approach of handcrafted feature extraction followed by a RF classifier. However, the high scores of a purely random classifier on this metric show how flawed it can be on unbalanced datasets. Instead, balanced accuracy (Kelleher et al. 2020) and metrics on plankton classes only both showed that CNN performed better in classifying objects, especially in low abundance classes (and when class weights were used). This was further confirmed by the fact that the difference between CNN and the classical approach was lower when classification was performed at a coarser taxonomic level. This makes the use of

450 pretrained CNN particularly relevant for plankton images classification, which are particularly diverse, contain many small classes and in which the dominant classes are often composed of various detritus and artifacts.

Giving more weight to poorly represented classes resulted in better performance, especially for RF. One plausible explanation would be that weighted RF (Chen et al. 2004) actually make use of class weights twice: weights are used to accurate the article accurate the accurate the article accurate the accurate the article accurate the article accurate the article accurate the accurate the article accurate the article accurate the accurate the

455 compute the criterion to generate the splits (entropy in our case) when building the tree; weights are also used when voting





for the majority class in terminal nodes. On the other hand, class weights are only used to compute a weighted loss in CNN (Cui et al. 2019).

While CNN took longer to train than RF in terms of overall training duration, the comparison is not straightforward. First, 460 training a RF model requires extracting features from the images beforehand. This feature extraction is coded, not trained, so this part cannot be directly compared. Additionally, it can be challenging to know when feature extraction is truly complete, as the optimal set of features often depends on the specific dataset and task. But even in terms of pure evaluation (i.e. extracting features and predicting the class of new images), the computation of some handcrafted features can take a nonnegligible amount of time and a CNN may prove faster, notably thanks to the use of GPUs by the underlying software libraries (Chellapilla et al. 2006). Additionally, the training time of CNN depends heavily on the number of parameters. For 465 instance, our lightweight model (MobileNet V2) trained in under 100 hours, which is fast compared to larger models (Zebin et al. 2019). Since lightweight CNN models demonstrated performance comparable to larger ones for plankton classification tasks, they present an appealing choice: their computational demands are often modest and compatible with most recent computers. Finally, a metric that may be more relevant than computational time for many applications is the total time 470 investment of the scientific team, including model setup, training, and output validation. In this respect, we argue that CNN are actually simpler: deep learning libraries such as Tensorflow (Abadi et al. 2016) or Pytorch (Paszke et al. 2019) are becoming easier to code in, no specific image processing knowledge is required to use them (while extracting relevant handcrafted features does require such skills), the final model packages the whole pipeline (from image pre-processing to

475 scientific community, these powerful tools become more accessible (Malde et al. 2020).

Finally, our results highlight the efficacy of both CNN and classical methods for accurate prediction of well-represented plankton classes. However, rare classes still require manual validation by a taxonomist. Importantly, improved prediction quality achieved by CNN compared to classical approaches is likely to save time by reducing the need for prediction corrections, as reported by Irisson et al. (2022).

classification) and can be deployed on various devices. And as GPU resources become increasingly available for the

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4.2 Importance of the quality and number of features

Models using a CNN feature extractor, which generated features much more numerous than the handcrafted ones (>1000 vs. ~50), performed better as expected from the literature (Orenstein and Beijbom 2017). Increasing the size of the feature extractor, hence yielding potentially richer features (keeping their number in the same order of magnitude: 1792 for the

MobileNet V2 vs. 1280 for the EfficientNet V2) did not lead to a significant improvement in classification performance; but 485 it did lengthen the training time. Reducing the number of features from a CNN to an amount similar to the number of handcrafted features (50), using PCA or compression within a small fully connected layer, did not significantly affect classification performance either. These results show that the richness and diversity of features is important, but only to a



certain extent with plankton images. Although features from CNN cannot be individually interpreted, texture features were shown to be important for image classification by CNN (Baker et al. 2018). Moreover, visualization techniques have been developed to provide insights into the convolutional layers of CNN, revealing that convolutional layers detect patterns like edges and textures (Zeiler and Fergus 2014). By contrast, most handcrafted feature sets were poor in texture-related features, which may explain their lower performance.

- 495 The fact that the number of features can be greatly reduced (from 1792 to 50, a 36-fold reduction, in our case; from 216 to 25, an 8-fold reduction, in Guo et al. 2021) suggests that CNN can only extract a limited amount of relevant information from plankton images, which are typically of small size (~100×100 pixels for the average Zooscan image) and often grayscale.
- 500 Therefore, improvements in classification accuracy are more likely to come from richer images than from larger models. For example, color cameras, such as those used in the planktoscope (Pollina et al. 2022) or the Scripps Plankton Camera (Orenstein et al. 2020b), should capture more information by using multiple channels. Beyond color, additional fluorescence channels can be obtained using environmental high content fluorescence microscopy, enriching the information content of images (Colin et al. 2017); but this method can only be applied ex situ. These enhanced imaging methods, however, require 505 greater storage and processing capacity. Our findings also opens an opportunity to simplify plankton image classification models, by performing a wise feature selection through recursive feature elimination for example (a backward selection of
- less informative features until only informative features remain; Guyon et al. 2002; Guo et al. 2021). Dimension reduction techniques, such as PCA (Legendre and Legendre 2012), can also be used to remove both correlations and noise in the features. The combination of deep feature extraction, dimension reduction, and a robust classifier, such as RandomForest, is
- 510 lightweight and quick to train, yet yields high quality results (Fig. 4). This approach is now implemented in the EcoTaxa web application (Picheral et al. 2017).

The similar performance between a full CNN and a deep feature extractor combined with a RF classifier (Fig. 4) suggests that the nature of the features is much more important than the nature of the classifier. These results are consistent with those

515 comparing different classifiers on handcrafted features, where no significant differences could be highlighted (Grosjean et al. 2004; Blaschko et al. 2005; Gorsky et al. 2010; Ellen et al. 2015). Still, in highly unbalanced datasets (IFCB, ISIIS and UVP6), the plankton precision was slightly higher with the RF than with the MLP₆₀₀, reflecting a lower contamination of plankton classes by dominant detritus. Its stronger sensitivity to class weights is another possible explanation in our case.

4.3 Alternative approaches for plankton image classification

520 A potential drawback of CNN is that they may not account for the real size of objects, since all images are rescaled to the same dimensions before input. One solution to capture size would be not to scale down images larger than the input





dimension but to pad the smaller ones with the background color. However, very small objects may be reduced to just 1 pixel after a few pooling layers and all information in the original image could be lost. Another common solution would be to concatenate size information from handcrafted features (e.g. area, Feret diameter) or simply the image diagonal size to one 525 of the fully connected layers to create a model that accounts for both image aspect and object size. Still, despite the a priori relevance of size to recognize plankton taxa, such approaches do not necessarily provide a large improvement in classification performance: Kerr et al. (2020) report a small improvement when geometric features are concatenated, while Kyathanahally et al. (2021) report a negligible gain. Ellen et al. (2019) evaluated the effect of concatenating different types of "metadata" (geometric, geotemporal and hydrographic) to fully connected layers; again, geometric features did not 530 improve model performance. One possible explanation is that deep features already capture the essential information needed for classification, making additional geometric features redundant. However, adding geotemporal and hydrographic features (individually or combined) enhanced prediction performance, which is unsurprising given the patchy nature of plankton organisms. Plankton taxa tend to exhibit positive correlations within groups (Greer et al. 2016; Robinson et al. 2021), and are often associated with specific environmental parameters—a relationship that machine learning algorithms can leverage (e.g., 535 relating plankton biomass to environmental conditions, as shown in Drago et al. 2022). However, one should keep in mind that incorporating metadata features during training may hinder subsequent analyses linking these organisms to their environment, since the classifier learned a correlation between the abundance of some organisms and some environmental

540 As highlighted above, plankton datasets are often highly unbalanced, with few objects in plankton classes while the largest classes often consist of non-living objects such as marine snow. There are both "algorithm-level" and "data-level" methods for dealing with class imbalance (Krawczyk 2016), which can be used separately or simultaneously. Algorithm-level methods include the use of class weights to give more importance to poorly represented classes in the loss computation (Cui et al. 2019); like we did here. Another algorithm-level method is to use a different loss function, such as sigmoid focal cross

conditions from the training set, and will therefore induce it in its predictions.

- 545 entropy (Lin et al. 2018), which penalizes hard examples (small classes) more than easier ones (large classes). We tested implementing focal cross entropy instead of a categorical cross entropy for our MobileNet V2, but it did not significantly change performance. Data-level methods include oversampling small classes and undersampling large classes, thereby rebalancing the distribution of classes in the training set (Krawczyk 2016). While this practice often improves performance on a test set to which the same modifications are applied, it can lead to poor performance when evaluating the model on a
- 550 real, therefore unbalanced, dataset, because the model has learned an unrepresentative class distribution from the training set. This problem is known as "dataset shift" (Moreno-Torres et al. 2012). Typically, using a model trained on an idealized training set to classify objects from a new, real dataset leads to poor prediction quality (González et al. 2017). Similarly, a model trained for specific conditions (such as location, depth, or time) may fail to generalize to images acquired under different circumstances. All types of classification models, including cutting-edge architectures like vision transformers, are



555 susceptible to dataset shift (Zhang et al. 2022). Today, there is no obvious solution to deal with dataset shift in classification tasks and other approaches, such as quantification, should be considered (González et al. 2019; Orenstein et al. 2020a).

The rarity of some plankton classes means that some classes will inevitably be missing in the training set. Since a classifier is trained with a fixed list of classes, all objects will be predicted in one of those classes and new, unknown, ones will be missed. In these situations, unsupervised or semi-supervised approaches, which can still exploit the rich features produced by

560 missed. In these situations, unsupervised or semi-supervised approaches, which can still exploit the rich features produced b CNN but do not target a fixed set of classes, may be preferable (Malde and Kim 2019; Schröder et al. 2020).

5 Conclusion and perspectives

In summary, a small CNN achieved strong performance at plankton image classification across six realistic plankton image datasets, while being easy to apply. It unsurprisingly outperformed the classical approach of extracting a small number of handcrafted features and using a RF classifier, particularly for rare classes. More specifically, the content of the features played a key role in driving these differences, while the choice of classifier had little impact. Surprisingly, using a large CNN did not lead to better classification performance than a much smaller one and that deep features could be quite heavily compressed without loss of performance. This is likely related to the fact that plankton images, which are typically small and grayscale, are poor in informative content for CNN. These findings suggest that improvements in imaging systems themselves could enhance classification performance. Finally, in agreement with previous findings, our work highlights the limitations of using global accuracy to evaluate classification performance on unbalanced datasets, such as plankton imaging

- datasets. Instead, metrics that emphasize the classes of interest often the minority classes in plankton datasets should be prioritized.
- 575 The results presented here are in line with the shift towards the use of deep learning models for plankton classification tasks (Rubbens et al. 2023), which was made possible by advances in computational performance through easier access to dedicated hardware, the release of sufficiently large datasets, and the development of turnkey deep learning libraries such as Tensorflow (Abadi et al. 2016) or Pytorch (Paszke et al. 2019). Datasets in this study are made publicly available to facilitate future benchmarking of new classification methods.

580 Data availability

The datasets used in this study are available online: IFCB (Sosik et al. 2015) at https://doi.org/10.1575/1912/7341; ISIIS (Panaïotis et al. 2024) at https://doi.org/10.17882/55741; FlowCAM (Jalabert et al. 2024) at https://doi.org/10.17882/101961; UVP6 (Picheral et al. 2024) at https://www.seanoe.org/data/00908/101948/; ZooCAM



(Romagnan et al. 2024) at https://doi.org/10.17882/101928; and ZooScan (Elineau et al. 2024) at 585 https://doi.org/10.17882/55741.

Code availability

All the code supporting this study is available at https://doi.org/10.5281/zenodo.15406618 (Panaïotis and Amblard 2025).

Author contribution

JOI and TP conceived the study; GBC and GDA developed a first CNN classifier; TP and EA implemented the RF classifier 590 and the final CNN classifier from the initial work of GBC and GDA, with guidance from BW; EA performed the experiments under the supervision of TP and JOI; TP wrote the original draft; all authors reviewed and approved the final manuscript.

Competing interests

Emma Amblard was employed by Fotonower. Guillaume Boniface-Chang was employed by Google Research, London. 595 Gabriel Dulac-Arnold was employed by Google Research, Paris. Ben Woodward was employed by CVision AI.

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References

610 Abadi, M. and others. 2016. TensorFlow: Large-Scale Machine Learning on Heterogeneous Distributed Systems. ArXiv160304467 Cs.

Anglès, S., A. Jordi, and L. Campbell. 2015. Responses of the coastal phytoplankton community to tropical cyclones revealed by high-frequency imaging flow cytometry. Limnol. Oceanogr. **60**: 1562–1576. doi:10.1002/lno.10117

Baker, N., H. Lu, G. Erlikhman, and P. J. Kellman. 2018. Deep convolutional networks do not classify based on global object shape. PLOS Comput. Biol. 14: e1006613. doi:10.1371/journal.pcbi.1006613

Benfield, M. and others. 2007. RAPID: Research on Automated Plankton Identification. Oceanography **20**: 172–187. doi:10.5670/oceanog.2007.63

Blaschko, M. B. and others. 2005. Automatic In Situ Identification of Plankton. 2005 Seventh IEEE Workshops on Applications of Computer Vision (WACV/MOTION'05) - Volume 1. Proceedings of the 2005 Seventh IEEE Workshops on

- Applications of Computer Vision (WACV/MOTION'05) Volume 1. 79–86.
 Breiman, L. 2001. Random Forests. Mach. Learn. 45: 5–32. doi:10.1023/A:1010933404324
 Chellapilla, K., S. Puri, and P. Simard. 2006. High Performance Convolutional Neural Networks for Document Processing.
 Proceedings of the Tenth International Workshop on Frontiers in Handwriting Recognition. Suvisoft.
 Chen, C., A. Liaw, and L. Breiman. 2004. Using Random Forest to Learn Imbalanced Data.
- 625 Cheng, K., X. Cheng, Y. Wang, H. Bi, and M. C. Benfield. 2019. Enhanced convolutional neural network for plankton identification and enumeration. PLOS ONE 14: e0219570. doi:10.1371/journal.pone.0219570
 Colas, F. and others. 2018. The ZooCAM, a new in-flow imaging system for fast onboard counting, sizing and classification of fish eggs and metazooplankton. Prog. Oceanogr. 166: 54–65. doi:10.1016/j.pocean.2017.10.014
 Colin, S., L. P. Coelho, S. Sunagawa, C. Bowler, E. Karsenti, P. Bork, R. Pepperkok, and C. de Vargas. 2017. Quantitative
- 630 3D-imaging for cell biology and ecology of environmental microbial eukaryotes P.G. Falkowski [ed.]. eLife 6: e26066. doi:10.7554/eLife.26066

Cowen, R. K., and C. M. Guigand. 2008. In situ ichthyoplankton imaging system (ISIIS): system design and preliminary results. Limnol. Oceanogr. Methods **6**: 126–132. doi:10.4319/lom.2008.6.126

Cowen, R. K., S. Sponaugle, K. L. Robinson, J. Luo, Oregon State University, and Hatfield Marine Science Center. 2015.

- PlanktonSet 1.0: Plankton imagery data collected from F.G. Walton Smith in Straits of Florida from 2014-06-03 to 2014-06-06 and used in the 2015 National Data Science Bowl (NCEI Accession 0127422).
 Cui, J., B. Wei, C. Wang, Z. Yu, H. Zheng, B. Zheng, and H. Yang. 2018. Texture and Shape Information Fusion of Convolutional Neural Network for Plankton Image Classification. *2018 OCEANS MTS/IEEE Kobe Techno-Oceans (OTO)*.
 Proceedings of the 2018 OCEANS MTS/IEEE Kobe Techno-Oceans (OTO). 1–5.
- 640 Cui, Y., M. Jia, T.-Y. Lin, Y. Song, and S. Belongie. 2019. Class-Balanced Loss Based on Effective Number of Samples. Proceedings of the Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition. 9268–9277.



Culverhouse, P. F. and others. 1996. Automatic classification of field-collected dinoflagellates by artificial neural network. Mar. Ecol. Prog. Ser. **139**: 281–287. doi:10.3354/meps139281

Dai, J., R. Wang, H. Zheng, G. Ji, and X. Qiao. 2016. ZooplanktoNet: Deep convolutional network for zooplankton classification. *OCEANS 2016 - Shanghai*. Proceedings of the OCEANS 2016 - Shanghai. 1–6.

Dai, J., Z. Yu, H. Zheng, B. Zheng, and N. Wang. 2017. A Hybrid Convolutional Neural Network for Plankton Classification. *Computer Vision – ACCV 2016 Workshops*. Springer International Publishing. 102–114.
Dieleman, S., J. De Fauw, and K. Kavukcuoglu. 2016. Exploiting Cyclic Symmetry in Convolutional Neural Networks. ArXiv160202660 Cs.

- Drago, L. and others. 2022. Global Distribution of Zooplankton Biomass Estimated by In Situ Imaging and Machine Learning. Front. Mar. Sci. 9. doi:10.3389/fmars.2022.894372
 Dyck, L. E. van, R. Kwitt, S. J. Denzler, and W. R. Gruber. 2021. Comparing Object Recognition in Humans and Deep Convolutional Neural Networks—An Eye Tracking Study. Front. Neurosci. 15: 750639. doi:10.3389/fnins.2021.750639
 Elineau, A. and others. 2018. ZooScanNet: plankton images captured with the ZooScan.doi:10.17882/55741
- 655 Elineau, A. and others. 2024. ZooScanNet: plankton images captured with the ZooScan.doi:10.17882/55741 Ellen, J., Hongyu Li, and M. D. Ohman. 2015. Quantifying California current plankton samples with efficient machine learning techniques. OCEANS 2015 - MTS/IEEE Washington. Proceedings of the OCEANS 2015 - MTS/IEEE Washington. 1–9.

Ellen, J. S., C. A. Graff, and M. D. Ohman. 2019. Improving plankton image classification using context metadata. Limnol.

- Oceanogr. Methods 17: 439–461. doi:10.1002/lom3.10324
 Falkowski, P. 2012. Ocean Science: The power of plankton. Nature 483: S17–S20. doi:10.1038/483S17a
 Fernández-Delgado, M., E. Cernadas, S. Barro, and D. Amorim. 2014. Do we need hundreds of classifiers to solve real world classification problems? J. Mach. Learn. Res. 15: 3133–3181.
 González, P., E. Álvarez, J. Díez, Á. López-Urrutia, and J. J. del Coz. 2017. Validation methods for plankton image
- classification systems. Limnol. Oceanogr. Methods 15: 221–237. doi:10.1002/lom3.10151
 González, P., A. Castaño, E. E. Peacock, J. Díez, J. J. Del Coz, and H. M. Sosik. 2019. Automatic plankton quantification using deep features. J. Plankton Res. 41: 449–463. doi:10.1093/plankt/fbz023
 Gorsky, G. and others. 2010. Digital zooplankton image analysis using the ZooScan integrated system. J. Plankton Res. 32: 285–303. doi:10.1093/plankt/fbp124
- 670 Greer, A. T., C. B. Woodson, C. E. Smith, C. M. Guigand, and R. K. Cowen. 2016. Examining mesozooplankton patch structure and its implications for trophic interactions in the northern Gulf of Mexico. J. Plankton Res. 38: 1115–1134. doi:10.1093/plankt/fbw033

Grosjean, P., M. Picheral, C. Warembourg, and G. Gorsky. 2004. Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system. ICES J. Mar. Sci. **61**: 518–525.

675 doi:10.1016/j.icesjms.2004.03.012

Springer Science & Business Media.



Guo, J., Y. Ma, and J. H. W. Lee. 2021. Real-time automated identification of algal bloom species for fisheries management in subtropical coastal waters. J. Hydro-Environ. Res. 36: 1–32. doi:10.1016/j.jher.2021.03.002
Guyon, I., and A. Elisseeff. 2003. An introduction to variable and feature selection. J. Mach. Learn. Res. 3: 1157–1182.
Guyon, I., J. Weston, S. Barnhill, and V. Vapnik. 2002. Gene Selection for Cancer Classification using Support Vector
Machines. Mach. Learn. 46: 389–422. doi:10.1023/A:1012487302797
Hastie, T., R. Tibshirani, and J. Friedman. 2009. The elements of statistical learning: data mining, inference, and prediction,

He, H., and E. A. Garcia. 2009. Learning from Imbalanced Data. IEEE Trans. Knowl. Data Eng. 21: 1263–1284. doi:10.1109/TKDE.2008.239

Hu, Q., and C. Davis. 2005. Automatic plankton image recognition with co-occurrence matrices and Support Vector Machine. Mar. Ecol. Prog. Ser. 295: 21–31. doi:10.3354/meps295021
Hutchinson, G. E. 1961. The Paradox of the Plankton. Am. Nat. 95: 137–145.
Irisson, J.-O., S.-D. Ayata, D. J. Lindsay, L. Karp-Boss, and L. Stemmann. 2022. Machine Learning for the Study of Plankton and Marine Snow from Images. Annu. Rev. Mar. Sci. 14: 277–301. doi:10.1146/annurev-marine-041921-013023

690 Jalabert, L., G. Signoret, L. Caray-Counil, M. Vilain, E. Martins, F. Lombard, M. Picheral, and J.-O. Irisson. 2024. FlowCAMNet: plankton images captured with the FlowCAM.doi:10.17882/101961 Kelleher, J. D., B. Mac Namee, and A. D'arcy. 2020. Fundamentals of machine learning for predictive data analytics: algorithms, worked examples, and case studies, MIT press.

Kerr, T., J. R. Clark, E. S. Fileman, C. E. Widdicombe, and N. Pugeault. 2020. Collaborative Deep Learning Models to

695 Handle Class Imbalance in FlowCam Plankton Imagery. IEEE Access 8: 170013–170032. doi:10.1109/ACCESS.2020.3022242

Krawczyk, B. 2016. Learning from imbalanced data: open challenges and future directions. Prog. Artif. Intell. **5**: 221–232. doi:10.1007/s13748-016-0094-0

Krizhevsky, A., I. Sutskever, and G. E. Hinton. 2012. ImageNet Classification with Deep Convolutional Neural Networks, p.

1097–1105. *In* F. Pereira, C.J.C. Burges, L. Bottou, and K.Q. Weinberger [eds.], Advances in Neural Information Processing Systems 25. Curran Associates, Inc.
 Kyathanahally, S. P., T. Hardeman, E. Merz, T. Bulas, M. Reyes, P. Isles, F. Pomati, and M. Baity-Jesi. 2021. Deep Learning Classification of Lake Zooplankton. Front. Microbiol. 12.

Kyathanahally, S. P., T. Hardeman, M. Reyes, E. Merz, T. Bulas, P. Brun, F. Pomati, and M. Baity-Jesi. 2022. Ensembles of

705 data-efficient vision transformers as a new paradigm for automated classification in ecology. Sci. Rep. 12: 18590. doi:10.1038/s41598-022-21910-0

LeCun, Y., B. Boser, J. Denker, D. Henderson, R. Howard, W. Hubbard, and L. Jackel. 1990. Handwritten digit recognition with a back-propagation network. Adv. Neural Inf. Process. Syst. **2**: 396–404.



Lee, H., M. Park, and J. Kim. 2016. Plankton classification on imbalanced large scale database via convolutional neural networks with transfer learning. 2016 IEEE International Conference on Image Processing (ICIP). Proceedings of the 2016 IEEE International Conference on Image Processing (ICIP). 3713–3717.

Legendre, P., and L. Legendre. 2012. Numerical ecology, Elsevier.

Lin, T.-Y., P. Goyal, R. Girshick, K. He, and P. Dollár. 2018. Focal Loss for Dense Object Detection. ArXiv170802002 Cs.

Lombard, F. and others. 2019. Globally Consistent Quantitative Observations of Planktonic Ecosystems. Front. Mar. Sci. 6. doi:10.3389/fmars.2019.00196

Lumini, A., and L. Nanni. 2019. Deep learning and transfer learning features for plankton classification. Ecol. Inform. **51**: 33–43. doi:10.1016/j.ecoinf.2019.02.007

Luo, J. Y., J.-O. Irisson, B. Graham, C. Guigand, A. Sarafraz, C. Mader, and R. K. Cowen. 2018. Automated plankton image analysis using convolutional neural networks. Limnol. Oceanogr. Methods **16**: 814–827. doi:10.1002/lom3.10285

720 Luo, T., K. Kramer, S. Samson, A. Remsen, D. B. Goldgof, L. O. Hall, and T. Hopkins. 2004. Active learning to recognize multiple types of plankton. *Proceedings of the 17th International Conference on Pattern Recognition, 2004. ICPR 2004.* Proceedings of the Proceedings of the 17th International Conference on Pattern Recognition, 2004. ICPR 2004. IEEE. 478-481 Vol.3.

Malde, K., N. O. Handegard, L. Eikvil, and A.-B. Salberg. 2020. Machine intelligence and the data-driven future of marine science. ICES J. Mar. Sci. **77**: 1274–1285. doi:10.1093/icesjms/fsz057

Malde, K., and H. Kim. 2019. Beyond image classification: zooplankton identification with deep vector space embeddings. ArXiv190911380 Cs.

Maracani, A., V. P. Pastore, L. Natale, L. Rosasco, and F. Odone. 2023. In-domain versus out-of-domain transfer learning in plankton image classification. Sci. Rep. **13**: 10443. doi:10.1038/s41598-023-37627-7

- 730 McCarthy, K., B. Zabar, and G. Weiss. 2005. Does cost-sensitive learning beat sampling for classifying rare classes? *Proceedings of the 1st international workshop on Utility-based data mining*. Association for Computing Machinery. 69–77. Moreno-Torres, J. G., T. Raeder, R. Alaiz-Rodríguez, N. V. Chawla, and F. Herrera. 2012. A unifying view on dataset shift in classification. Pattern Recognit. 45: 521–530. doi:10.1016/j.patcog.2011.06.019 Ohman, M. D., R. E. Davis, J. T. Sherman, K. R. Grindley, B. M. Whitmore, C. F. Nickels, and J. S. Ellen. 2019. Zooglider:
- An autonomous vehicle for optical and acoustic sensing of zooplankton. Limnol. Oceanogr. Methods 17: 69–86. doi:10.1002/lom3.10301
 Olson, R. J., and H. M. Sosik. 2007. A submersible imaging-in-flow instrument to analyze nano-and microplankton: Imaging FlowCytobot. Limnol. Oceanogr. Methods 5: 195–203. doi:10.4319/lom.2007.5.195

Orenstein, E. C. and others. 2022. Machine learning techniques to characterize functional traits of plankton from image data. 740 Limnol. Oceanogr. **67**: 1647–1669. doi:10.1002/lno.12101



745

Orenstein, E. C., and O. Beijbom. 2017. Transfer Learning and Deep Feature Extraction for Planktonic Image Data Sets. 2017 IEEE Winter Conference on Applications of Computer Vision (WACV). Proceedings of the 2017 IEEE Winter Conference on Applications of Computer Vision (WACV). 1082–1088.

Orenstein, E. C., O. Beijbom, E. E. Peacock, and H. M. Sosik. 2015. WHOI-Plankton- A Large Scale Fine Grained Visual Recognition Benchmark Dataset for Plankton Classification. ArXiv151000745 Cs.

Orenstein, E. C., K. M. Kenitz, P. L. D. Roberts, P. J. S. Franks, J. S. Jaffe, and A. D. Barton. 2020a. Semi- and fully supervised quantification techniques to improve population estimates from machine classifiers. Limnol. Oceanogr. Methods **18**: 739–753. doi:10.1002/lom3.10399

Orenstein, E. C., D. Ratelle, C. Briseño-Avena, M. L. Carter, P. J. S. Franks, J. S. Jaffe, and P. L. D. Roberts. 2020b. The

750 Scripps Plankton Camera system: A framework and platform for in situ microscopy. Limnol. Oceanogr. Methods 18: 681– 695. doi:10.1002/lom3.10394

Panaïotis, T. and others. 2022. Content-Aware Segmentation of Objects Spanning a Large Size Range: Application to Plankton Images. Front. Mar. Sci. 9. doi:10.3389/fmars.2022.870005

```
Panaïotis, T., and E. Amblard. 2025. ThelmaPana/plankton_classif: Updated results for submission.doi:10.5281/zenodo.15406618
```

Panaïotis, T., L. Caray-Counil, L. Jalabert, and J.-O. Irisson. 2024. ISIISNet : plankton images captured with the ISIIS (Insitu Ichthyoplankton Imaging System).doi:10.17882/101950

Paszke, A. and others. 2019. PyTorch: An Imperative Style, High-Performance Deep Learning Library.doi:10.48550/arXiv.1912.01703

- Pedregosa, F. and others. 2011. Scikit-learn: Machine Learning in Python. J. Mach. Learn. Res. 12: 2825–2830.
 Péron, F., and C. A. Lesueur. 1810. Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce jour. *Annales du Muséum d'Histoire Naturelle*. 325–366.
 Picheral, M. and others. 2021. The Underwater Vision Profiler 6: an imaging sensor of particle size spectra and plankton, for autonomous and cabled platforms. Limnol. Oceanogr. Methods n/a. doi:10.1002/lom3.10475
- Picheral, M., S. Colin, and J.-O. Irisson. 2017. EcoTaxa, a tool for the taxonomic classification of images.
 Picheral, M., L. Courchet, L. Jalabert, S. Motreuil, L. Carray-Counil, F. Ricour, and F. Petit. 2024. UVP6Net : plankton images captured with the UVP6.doi:10.17882/101948
 Picheral, M., L. Guidi, L. Stemmann, D. M. Karl, G. Iddaoud, and G. Gorsky. 2010. The Underwater Vision Profiler 5: An advanced instrument for high spatial resolution studies of particle size spectra and zooplankton. Limnol. Oceanogr. Methods
 8: 462–473. doi:10.4319/lom.2010.8.462
- Pollina, T., A. G. Larson, F. Lombard, H. Li, D. Le Guen, S. Colin, C. de Vargas, and M. Prakash. 2022. PlanktoScope: Affordable Modular Quantitative Imaging Platform for Citizen Oceanography. Front. Mar. Sci. 9.

9: 671–675. doi:10.1038/nmeth.2089



 Py, O., H. Hong, and S. Zhongzhi. 2016. Plankton classification with deep convolutional neural networks. 2016 IEEE Information Technology, Networking, Electronic and Automation Control Conference. Proceedings of the 2016 IEEE
 775 Information Technology, Networking, Electronic and Automation Control Conference. 132–136.

Raghu, M., T. Unterthiner, S. Kornblith, C. Zhang, and A. Dosovitskiy. 2021. Do Vision Transformers See Like Convolutional Neural Networks? *Advances in Neural Information Processing Systems*. Curran Associates, Inc. 12116–12128.

Robinson, K. L., S. Sponaugle, J. Y. Luo, M. R. Gleiber, and R. K. Cowen. 2021. Big or small, patchy all: Resolution of

- marine plankton patch structure at micro- to submesoscales for 36 taxa. Sci. Adv. 7: eabk2904. doi:10.1126/sciadv.abk2904
 Rodrigues, F. C. M., N. S. Hirata, A. A. Abello, T. Leandro, D. La Cruz, R. M. Lopes, and R. Hirata Jr. 2018. Evaluation of Transfer Learning Scenarios in Plankton Image Classification. *VISIGRAPP (5: VISAPP)*. 359–366.
 Romagnan, J.-B. and others. 2024. ZooCAMNet : plankton images captured with the ZooCAM.doi:10.17882/101928
 Rubbens, P. and others. 2023. Machine learning in marine ecology: an overview of techniques and applications. ICES J.
- Mar. Sci. 80: 1829–1853. doi:10.1093/icesjms/fsad100
 Russakovsky, O. and others. 2015. ImageNet Large Scale Visual Recognition Challenge. Int. J. Comput. Vis. 115: 211–252. doi:10.1007/s11263-015-0816-y
 Sandler, M., A. Howard, M. Zhu, A. Zhmoginov, and L.-C. Chen. 2019. MobileNetV2: Inverted Residuals and Linear Bottlenecks. ArXiv180104381 Cs.
- 790 Schmid, M. S., R. K. Cowen, K. Robinson, J. Y. Luo, C. Briseño-Avena, and S. Sponaugle. 2020. Prey and predator overlap at the edge of a mesoscale eddy: fine-scale, in-situ distributions to inform our understanding of oceanographic processes. Sci. Rep. 10: 1–16. doi:10.1038/s41598-020-57879-x Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods
- Schröder, S.-M., R. Kiko, J.-O. Irisson, and R. Koch. 2019. Low-Shot Learning of Plankton Categories. *Pattern Recognition*. Springer International Publishing. 391–404.
 Schröder, S.-M., R. Kiko, and R. Koch. 2020. MorphoCluster: Efficient Annotation of Plankton Images by Clustering. Sensors 20: 3060. doi:10.3390/s20113060
- Ser-Giacomi, E., L. Zinger, S. Malviya, C. De Vargas, E. Karsenti, C. Bowler, and S. De Monte. 2018. Ubiquitous
 abundance distribution of non-dominant plankton across the global ocean. Nat. Ecol. Evol. 2: 1243–1249. doi:10.1038/s41559-018-0587-2

Shorten, C., and T. M. Khoshgoftaar. 2019. A survey on Image Data Augmentation for Deep Learning. J. Big Data 6: 60. doi:10.1186/s40537-019-0197-0

Sieracki, C. K., M. E. Sieracki, and C. S. Yentsch. 1998. An imaging-in-flow system for automated analysis of marine microplankton. Mar. Ecol. Prog. Ser. **168**: 285–296. doi:10.3354/meps168285



Smith, L. N. 2018. A disciplined approach to neural network hyper-parameters: Part 1 -- learning rate, batch size, momentum, and weight decay.doi:10.48550/arXiv.1803.09820

Soda, P. 2011. A multi-objective optimisation approach for class imbalance learning. Pattern Recognit. 44: 1801–1810. doi:10.1016/j.patcog.2011.01.015

- Sosik, H. M., and R. J. Olson. 2007. Automated taxonomic classification of phytoplankton sampled with imaging-in-flow cytometry. Limnol. Oceanogr. Methods 5: 204–216. doi:10.4319/lom.2007.5.204
 Sosik, H. M., E. E. Peacock, and E. F. Brownlee. 2015. WHOI-Plankton. Annotated Plankton Images Data Set for Developing and Evaluating Classification Methods.
 Srivastava, N., G. Hinton, A. Krizhevsky, I. Sutskever, and R. Salakhutdinov. 2014. Dropout: a simple way to prevent neural
- 815 networks from overfitting. J. Mach. Learn. Res. 15: 1929–1958.
 Sun, Y., A. K. C. Wong, and M. S. Kamel. 2009. Classification of imbalanced data: a review. Int. J. Pattern Recognit. Artif. Intell. 23: 687–719. doi:10.1142/S0218001409007326
 Tan, M., and Q. Le. 2021. EfficientNetV2: Smaller Models and Faster Training. *Proceedings of the 38th International Conference on Machine Learning*. Proceedings of the International Conference on Machine Learning. PMLR. 10096–10106.
- Tang, X., W. K. Stewart, H. Huang, S. M. Gallager, C. S. Davis, L. Vincent, and M. Marra. 1998. Automatic Plankton Image Recognition. Artif. Intell. Rev. 12: 177–199. doi:10.1023/A:1006517211724
 Tappan, H., and A. R. Loeblich. 1973. Evolution of the oceanic plankton. Earth-Sci. Rev. 9: 207–240. doi:10.1016/0012-8252(73)90092-5

Uchida, K., M. Tanaka, and M. Okutomi. 2018. Coupled convolution layer for convolutional neural network. Neural Netw. **105**: 197–205. doi:10.1016/j.neunet.2018.05.002

- Van Horn, G., and P. Perona. 2017. The Devil is in the Tails: Fine-grained Classification in the Wild. ArXiv170901450 Cs.
 Vaswani, A., N. Shazeer, N. Parmar, J. Uszkoreit, L. Jones, A. N. Gomez, Ł. Kaiser, and I. Polosukhin. 2017. Attention is All you Need. *Advances in Neural Information Processing Systems*. Curran Associates, Inc.
 Walt, S. van der, J. L. Schönberger, J. Nunez-Iglesias, F. Boulogne, J. D. Warner, N. Yager, E. Gouillart, and T. Yu. 2014.
- scikit-image: image processing in Python. PeerJ 2: e453. doi:10.7717/peerj.453
 Ware, D. M., and R. E. Thomson. 2005. Bottom-Up Ecosystem Trophic Dynamics Determine Fish Production in the Northeast Pacific. Science 308: 1280–1284. doi:10.1126/SCIENCE.1109049
 Yosinski, J., J. Clune, Y. Bengio, and H. Lipson. 2014. How transferable are features in deep neural networks? ArXiv14111792 Cs.
- 835 Zebin, T., P. J. Scully, N. Peek, A. J. Casson, and K. B. Ozanyan. 2019. Design and Implementation of a Convolutional Neural Network on an Edge Computing Smartphone for Human Activity Recognition. IEEE Access 7: 133509–133520. doi:10.1109/ACCESS.2019.2941836

Zhang, C. and others. 2022. Delving Deep into the Generalization of Vision Transformers under Distribution Shifts.doi:10.48550/arXiv.2106.07617





840 Zheng, H., R. Wang, Z. Yu, N. Wang, Z. Gu, and B. Zheng. 2017. Automatic plankton image classification combining multiple view features via multiple kernel learning. BMC Bioinformatics 18: 570. doi:10.1186/s12859-017-1954-8